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Biological background for the development of a new fishery for the grooved Tanner crab (*Chionoecetes tanneri*) of British Columbia

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Abstract

This paper reviews what is known of the biology and fishery for the Grooved Tanner crab, *Chionoecetes tanneri* as the first phase towards developing a new fishery for this species. Specific information was collected from past and present fisheries for this species and fisheries that recorded *C tanneri* as bycatch. Additional information from research activities and museum collections is also included. Literature on life histories and fisheries for related species is extensively reviewed and applicability of this information to a potential fishery for *C. tanneri* is considered.

The stock(s) of *C. tanneri* are not presently well defined, however it appears that no other fisheries have as yet had a significant impact on stocks due to this species deep distribution (>500m). As a result, any directed fishing will impact a virgin biomass. Information collected at the beginning phase of this fishery will be of extreme importance in subsequent stock assessment and management. From our review of other and similar fisheries, it appears likely that *C. tanneri* cannot be managed on the basis of size and sex limitation alone. Aspects of the life history and reproductive process should be considered in developing a risk-averse harvest strategy.

Résumé

Le document résume les connaissances actuelles sur la biologie et la pêche du crabe Tanner, *Chionoecetes tanneri*, dans l'optique d'une nouvelle pêche de cette espèce. Les renseignements ont été obtenus à partir de pêches, actuelles ou antérieures, de cette espèce et de pêches où ce crabe est capturé de façon accidentelle. On trouve aussi d'autres renseignements provenant de recherches ou de collections de musée. Les publications sur le cycle vital et les pêches d'espèces apparentées sont traitées de façon approfondie et l'on examine l'application éventuelle de ces informations à une pêche de *C. tanneri*.

Le ou les stocks de *C. tanneri* ne sont pas bien définis, mais il semble qu'aucune autre pêche n'ait eu d'effet appréciable sur ces stocks étant donné l'importante profondeur où se trouve ce crabe (plus de 500 m). Toute pêche porterait donc sur une biomasse vierge. Les renseignements recueillis au début d'une telle pêche présenteraient une très haute importance pour l'évaluation et la gestion ultérieures des stocks. Il apparaît, selon notre examen d'autres pêches, que *C. tanneri* ne pourrait être géré exclusivement par des limites visant la taille ou le sexe. Les caractéristiques du cycle vital et du processus reproductif devraient être prises en compte au moment de l'élaboration d'une stratégie de récolte prudente.

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FISHERY DEVELOPMENT

POLICY ON NEW FISHERIES

Due to growing concerns about the overharvest of fish and invertebrate stocks, and lack of biological information with which to manage them, the Department of Fisheries and Oceans, in 1990, placed a moratorium on the development of any new fisheries or new fishing technologies until criterion for controlled exploitation could be developed. Subsequently, upwards of 24 potential new invertebrate fisheries have been identified. The Flying squid, Venus clam, Pacific mackerel and the Deepwater or Grooved Tanner crab were selected as having the most immediate potential. Only the fishery for flying squid has begun to date. Fishing and management plans have yet to be developed for the other species. This paper is part of that process for the Tanner crab *Chionoecetes tanneri*. Other related crab species are not directly considered here.

GOALS FOR THE DEVELOPMENT OF A NEW FISHERY

The goals for establishing a fishery for Tanner crabs (or any new fishery) as stated in the Memorandum of Understanding between the Federal Government of Canada and the Provincial Government of British Columbia signed in December 1995 are to:

(a) diversify British Columbia fisheries and seafood production to ensure conservation of stocks and realize the optimal sustainable use of fisheries resources and fish culture;
(b) encourage a competitive business approach to fisheries and aquaculture diversification, and maximize marketing opportunities;
(c) diversify the seafood sector in British Columbia to promote employment opportunities, foster community development and secure social and economic stability;
(d) encourage public and private sector cooperation in fisheries diversification, including new arrangements between regional communities, harvesters and growers.

BIOLOGICAL OBJECTIVES

Broadly stated, the biological objective for a fishery for *C. tanneri* is to maintain a viable, healthy and productive stock throughout its natural range in British Columbia. Specific objectives for Tanner crabs are derived from the PSARC report tabled in 1994. (Rice et al. 1995) These are to:

1. Ensure that the populations (sub-populations) of Tanner crabs along the British Columbia coast do not become biologically threatened throughout their ecological range.

2. Ensure production of sufficient progeny, after accounting for all sources of mortality, to reproduce the population(s) throughout their ecological range.

3. Ensure that a fishery for Tanner crab does not violate the above two objectives for other ecologically related species.

Incumbent in this process is the collection of sufficient biological data to determine a safe (in terms of risk averse) level of harvest and to be able to detect changes to the stock dynamics from any cause in time to prevent long term decline or collapse of the stock through over-exploitation.

PLAN FOR THE DEVELOPMENT OF A NEW FISHERY FOR TANNER CRABS

The proposed framework for development of the Tanner crab fishery involves three "phases" of activities required to develop this fishery in a precautionary manner. These are described in detail in Perry et al.. (1997 submitted for review). Briefly summarized, these are:

Phase 0. Summarization of all known biological, distributional and fisheries related information on the target species and from similar species from similar habitats. A thorough review of the literature and all available data sources should provide some of the basic parameters referred to above and suggest appropriate management strategies.

Phase 1. A limited fishery in order to acquire information lacking in phase 0; to test or develop management strategies and to determine the feasibility of a fishery.

Phase 2. Fishery development at the commercial level while monitoring stocks and evaluating management strategies.

This paper constitutes the Phase 0 review of known and derived information concerning *Chionocetes tanneri.*

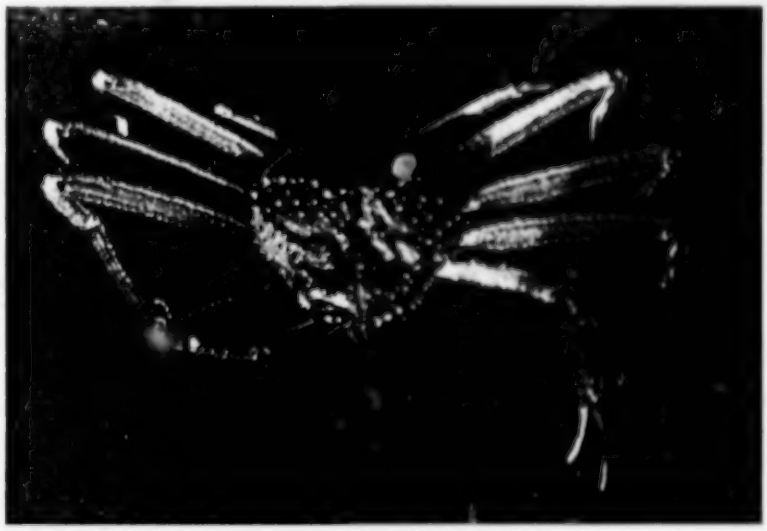
OUR CURRENT KNOWLEDGE OF *CHIONOECETES TANNERI*

BIOLOGY AND LIFE HISTORY

General description

The Grooved Tanner crab, *Chionoecetes tanneri*, is a large deep-water spider crab. It is a member of the Family Majidae or true crabs identified by having 4 sets of walking legs and 2 claws (unlike Lithodid or king crabs, which have only 3 pairs of walking legs). The species was first described by Rathbun in 1893 from the Farallone Islands, California in

29 fathoms (Rathbun, 1925). The crab (Fig. 1&2) resembles other spider crabs of the genus *Chionoecetes*, but is noted for its scarlet colour, deep chocolate eye colour, and the enlarged branchial lobes of the carapace with a deep groove between them (from which it derives its common name). The legs are longer and thinner than those of the Snow crab (*Chionoecetes opilio*) or the Alaskan Tanner (*C. bairdi*). It most closely resembles the other deepwater crab of the same genus, *C. angulatus* or Angle Tanner. The Angle Tanner is also scarlet (except for juveniles which are white) but can be distinguished by the angle formed by the spines on the carapace, hence its common name. Adult male *C. tanneri* are about 140-160 mm in carapace width (CW) and weigh about 500-900 g, and females are about 100-120mm CW and weigh about 300-500 g. Carapace width is slightly greater than carapace length for this species.



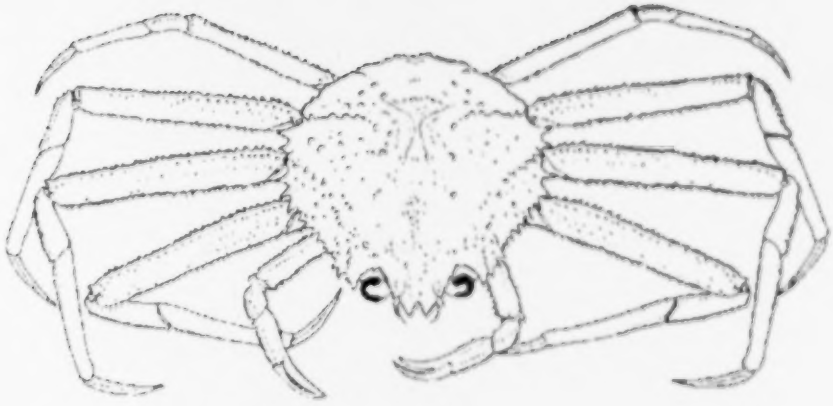


Figure 1: Photograph of male Tanner crab (Chionoecetes tanneri).

Figure 2: Line drawing of immature male Grooved Tanner crab (Hart 1982)

DISTRIBUTION

Geographic Range

C. tanneri are unique to the western Pacific where they occur from Mexico to the Gulf of Alaska at depths ranging from 53-1,944 m (Rathbun, 1925;Pereyra 1968; Hart 1982). In B.C. they are known from 458-1,784 m (Hart 1982). Their theoretical bathymetric distribution is a narrow ribbon bounded by these depths along the continental slope (Jamieson 1989). They are not known from coastal inlets as are *C. bairdi* (Jamieson et al. 1986), although they occur on some offshore seamounts off British Columbia and the Gulf of Alaska over similar depth strata to the continental slope populations (Jamieson 1990; Hughes 1981; Alton 1986).

A small fishery for *C. tanneri* took place during 1988 and 1989 off the west coast of Vancouver Island. There was insufficient effort during the brief period of the fishery to document spatial distribution except for some specific locations off Tofino and Nootka Sound. Little is known of their distribution in the northern part of their range in British Columbia .

Sablefish fishers sporadically report them as bycatch in their traps although commercial fishing depth of sablefish (*Anoplopoma fimbria*) is near the upper depth range of commercial distributions of Tanner crabs (Murie et al. 1995, Jamieson 1990). They have been recorded during the course of some Sablefish stock assessment surveys (Smith et al. 1996,) It is probable that much of the bycatch of this species goes unreported (Heritage 1997, pers.com., Griffiths and Edwards 1988,89 pers. com.). Recent data indicate distribution is coastwide but is insufficient to determine if this is a single population or a series of discrete stocks.

Exploratory trawling for slope rockfish took place during 1996 with observer coverage. Information from this survey (unpublished) produced a relatively minor bycatch of Tanner crabs, but trawl depths again were near the upper depth range of the Tanner crab distribution.

The Provincial Museum of British Columbia has, over the years, made a series of collections by trawl over the slope region (Figure 3). Tanner crabs were reported from their catches from 460 m to 1,020 m (courtesy Lambert 1997, unpublished data).

A recent sablefish survey conducted in May, 1997 (results unpublished) in which bycatch was accurately identified and reported by Dwight Heritage, catch observer, previously of DFO and involved in initial work with Tanner crabs here, filled in many of the gaps in the above museum records and demonstrated coastwide distribution. Data from both sources are included in the distributional map below.

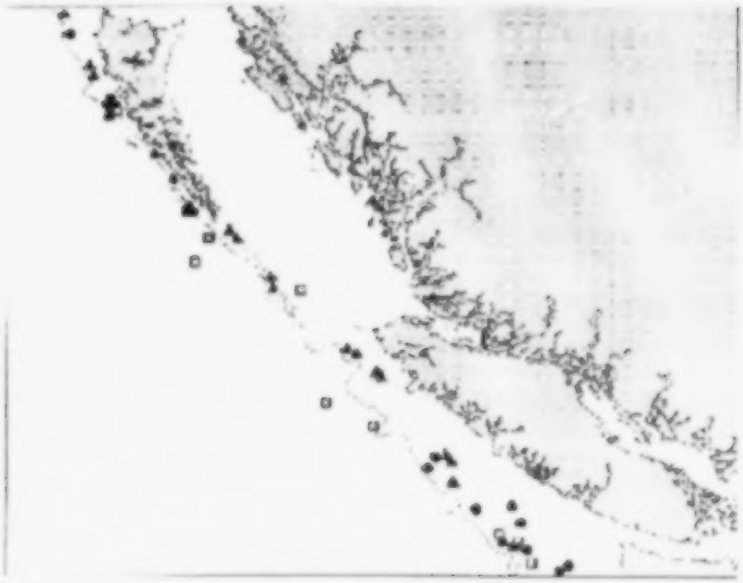


Figure 3: Records of C. tannero (circles) and C. angulatus (squares) from the Provincial Museum of British Columbia collections (unpublished), and from a recent sablefish survey (triangles-Heritage 1997, pers.com.)

Bathymetric and Seasonal Distribution

Fishing during 1988 and 1989 off Vancouver Island took place at depths between 400 and 700 m, with the major abundance of large males occurring in about 550 m. A research cruise made in conjunction with the fishery during 1988 (Jamieson et al. 1990) found crabs from 325 to 770 m.

Trawl surveys off the mouth of the Columbia River between 1961 and 1964 (Pereyra 1967, 1968) documented bathymetric distribution of *C. tanneri* by sex, season and life stages. Absolute depth range in this study was from 250 to 1,050 fm (457-1920 m) with the bulk of the adult population occurring between 450 and 700 m. Segregation by sex was observed during most of the year. The adult male population was centered between 500 and 640 m while females occupied a deeper zone between 640 and 690 m. As winter approached, males shifted their distribution downslope to correspond to that of the females . By early spring the two populations overlapped, presumably for the purpose of breeding and then segregated once more with the approach of summer.

The sub-adult distribution ranged from 594 to 1,920 m with the center of abundance from 640 to 1,463 m which is deeper than that for the adults. Newly settled and immature crabs were found deeper than juveniles and it was therefore assumed that recruitment occurred ontogenetically from depth.

Segregation by sex and life stage occurs off the coast of British Columbia (Jamieson 1990). The adult male distribution appears to be 580-670 m while adult females occupy the strata between 670-720 m. Juveniles occur below the female distribution at 720-1,100 m. The fishing season during the two years in which it occurred targeted hard shell male crabs over 110 mm (Jamieson 1990) and took place during the winter and early spring. Fishing terminated when females became overwhelmingly abundant in the traps, which occurred in late spring (Jamieson 1990, Griffiths and Edwards, pers. comm.). This phenomenon suggests a migration of females, which normally occupy deeper water than the males during breeding season (Jamieson 1990a), the reverse of what was documented by Pereyra (1967).

In Alaska, *C. tanneri* are fished from 400 to 900 m along the Aleutian chain and in the Bering Sea. Commercial fishing depth appears to be about 650 - 750 m. Somerton and Donaldson (1996) from a trawl survey of the eastern Bering Sea, report the mean depth distribution for mature *C. tanneri* to be 752 m for males and 709 m for females, which was not considered to be significantly different. No segregation by sex was observed and overall distribution in this study was deeper than that observed to the south (580-720 m Jamieson 1990, 549-640 m Pereyra 1967). In addition, juvenile *C. tanneri* were captured in shallower water than adults, opposite to what was observed off British Columbia (Jamieson 1990) and Oregon (Pereyra 1967).

BOTTOM TYPE ASSOCIATED WITH TANNER DISTRIBUTIONS

Hart (1982) gives the habitat of *C. tanneri* as deep water green mud, fine sand and rocks. Catch data reports green mud for some samples off Vancouver Island. Jamieson (1990) found *C. tanneri* trapped on Union Seamount to be more abundant on soft bottom with a lesser slope than rockier slope areas. Pereyra (1967) describes the sediment type associated with *C. tanneri* to range from sandy silt to silty clay; however all sites along his trackline were trawlable and other bottom types were not sampled or did not exist over the area surveyed. Tanner crabs appear to favour fine sediments as opposed to courser bottoms.

Sediment type over the lower continental slope region varies from silt to cobble and rock. The bottom type in the area in which crabs were harvested in 1988-1989 is predominantly sandy silt, similar to the habitat described off the Columbia River (Pereyra 1966). It would appear that bottom type characteristic of *C. tanneri* records predominates over most of their range in British Columbia (unpublished data records, Pacific Geoscience Centre, courtesy B. Bornhold). Fine-scale differences are noted in some adjacent samples. The degree to which bottom type influences distribution is yet to be determined.

PHYSIOLOGY, FOOD AND FEEDING

C. tanneri is a little-studied, deep-water species for which little is known about physiological adaptations or environmental requirements beyond enlarged branchial lobes on the carapace to accommodate a larger gill mass than shallow water counterparts. This is presumably an adaptation to deep water, low oxygen availability (Somerton 1981). Their bright orange coloration is typical of intermediate depth invertebrates where red light is absorbed by the water rendering them less visible. Nothing is known of their caloric intake or metabolic requirements or of their resistance to changes in temperature and pressure as a result of capture and stresses involved by exposure to air and subsequent release in warmer surface waters Preliminary evidence suggests they are quite susceptible to changes in salinity and exposure to warm (>10° C) water (Edwards, pers. com.). Survival appeared best when crabs were sprayed with refrigerated oceanic seawater rather than held submerged. Off the west coast of Vancouver Island surface temperatures near 7°C are predominate. However, around offshore seamounts surface water temperatures above 18°C were encountered due to influence of warm subtropical water (Jamieson 1990).

Their diet has not been studied. In aquaria, they were observed to feed on brittle stars, fish pellets and pieces of herring. It is reasonable to assume that they feed on benthic invertebrates for the most part including amphipods, copepods, ophiuroids, clams, worms and detritus. They may be cannibalistic and are undoubtedly opportunists, feeding on fish carcasses and other large pieces of carrion that settle on the bottom. They are attracted to traps baited with herring, squid, hake and various fish offal, however the range over which attraction occurs is not known.

REPRODUCTION

Pereyra (1967) documented the reproductive life history of *C. tanneri* off the mouth of the Columbia River in Oregon. As noted above, he describes a mating migration of males to deeper water where females occur throughout the year. His observations indicated that the release of eggs, molting and mating took place during early spring. Reproduction appeared to take place on an annual cycle with release of eggs prerequisite to breeding in female crabs. Somerton and Donaldson (1996) also found that reproduction was synchronous and annual. They give mean fecundity as 86,500 eggs per female, which did not increase with carapace width. Mean egg diameter was 0.74 mm from their observations.

It is assumed that larvae, when released, make their way to surface waters where they feed and eventually transform and settle as juvenile crabs. The process is not documented. It is hypothesized (Pereyra 1967) that larvae occupy surface waters during the late spring and summer where they are transported by surface currents. Newly settled benthic juveniles were found below the depth of adult crabs (Pereyra, 1967) from which he concluded recruitment to the adult population occurred. Jamieson (1990) also found juvenile distribution below that of the adults. Somerton and Donaldson (1996)

however found juveniles distributed in shallower water than the adults. The difference they suggest may be due to local oceanographic conditions.

SIZE DISTRIBUTION, AGE AND GROWTH

Little is known about growth rates or the age structure for this species. Size distribution from samples taken off Vancouver Island (unpublished data used in Jamieson 1990; Jamieson et al. 1990) are 100-174 mm for males and 96-138 mm for females. Modal male length in the trap fishery was 137 mm and 116 mm for males and females respectively. Due to limited data and lack of immature male crabs in samples, no calculation of size at maturity was made from these data (Jamieson 1990).

In samples from the 1995 commercial trap fishery in Alaska (Pengilly 1996 unpublished data), male CW ranged from about 90 to 180 mm with an average size of 125 to 140 mm depending on area (Boyle et al. 1996). Females ranged from about 80 to 115 mm averaging approximately 95 mm in the South Peninsula region to about 105 mm in the Bering Sea. Size distribution from 1994 Bering sea commercial samples (1995-1996) ranged from approx. 121 to 170 mm for males with an average width of 136 mm. Females in this fishery ranged from 75-125mm CW with an average width of 102 mm. A trawl survey from the eastern Bering Sea in 1982 (Somerton and Donaldson 1996) give a size range for males of 42-170mm and 38-126mm for females, with mean carapace widths are about 136 mm and 97 mm for males and females respectively. Pereyra (1966) calculated 148.9 mm and 102.5 mm for crabs off northern Oregon.

Estimates of size at 50% maturity of 118.7 and 79.2 mm for males and females respectively were obtained by Somerton and Donaldson (1996). They also give mean size at maturity of 137.9 mm for males and 99.5 mm for females, noting that these values are remarkably consistent throughout the range of *Chionoecetes tanneri*. Tester and Carey's (1986) CW measurements at 50% maturity were 142.7 mm and 102.3 mm for males and females respectively. No similar values are available for British Columbia.

Both sexes of *C. tanneri* exhibit allometry associated with functional maturity in congeners, the female by a marked increase in the width of the third abdominal segment; the male by a change in claw size with respect to body size. Jamieson (1989) presents two equations which separate functionally mature from immature male crabs based on the ratios of shell width or shell length on chela length. Samples were from the west coast of Vancouver Island.

MC = log(chela length - 1.41 log(min CW) + 2.92 and
MC = log(chela length - 1.47 log(min CL) + 3.11
where MC=Maturity Code; CW = carapace width and CL = carapace length.

A positive value indicates a mature crab.

Difficulty was encountered in aging adult crabs in the Alaska fishery due to lack of shell abrasion and epiphytic growth in mature males (Pengilly 1996), which were usually

classed as new shell, having molted within the preceding 12 months. Female crabs were nearly always classed as old shell. These findings are consistent with those of Pereyra (1967). Both authors suggest that a terminal molt probably occurs in females but may not occur in males. Crabs sampled off Vancouver Island contained both obviously old shelled individuals as well as new molts of both sexes; however, males were predominantly new shelled, whereas females were predominantly old shell. Soft-shelled males were rare, possibly due to spatial isolation or avoidance behavior during the molting period.

POPULATION DYNAMICS

The fishery for deep water Tanner crabs is a relatively new fishery in Alaska and Oregon and does not exist elsewhere. Consequently little is known of population dynamics, long term trends in abundance, or fluctuations in recruitment. Most data is from pot samples which do not adequately sample smaller crabs. In Alaska, fishing effort and landed value increased to 1995 but declined dramatically during 1996 for several reasons (Pengilly 1996). Regulations for the 1997 fishery in Alaska reflect concern for the stocks (ADF&G news release, 25 Feb. 1997).

PREDATORS, PARASITES AND DISEASES

Predation on *C. tanneri* probably occurs at some stage by all of the larger flatfish, roundfish and invertebrate species listed in Table 1 (below). Tester and Carey (1986) obtained early instars from the stomachs of Dover sole (*microstomus pacificus*) and sablefish (*Anoplopoma fimbria*). In addition, larger crabs are possibly cannibalistic on smaller crabs and may even consume larger newly molted soft crabs. The formation of large aggregations of individuals for protection and/or reproduction as seen in other species of Tanner and King crabs has not been reported.

No parasites or diseases are described for this species although they are probably susceptible to some that are described for *C. bairdi* and *C. opilio*.(see discussion below)

FISHERIES FOR *C. TANNERI*

History

A small fishery developed for *Chionoecetes tanneri* off British Columbia in 1988 and 1989 as a result of incidental bycatch in the sablefish trap fishery . Exploratory fishing took place under scientific permit issued by the Canadian Department of Fisheries and Oceans and was prosecuted by only two vessels which fished exclusively off the west coast of Vancouver Island, primarily during the late winter and spring of those two years (Jamieson 1990). Catch was landed and processed locally, with the main market Japan. Fishing terminated due to low prices for product as a consequence of high landings *of C. bairdi* from Alaska and an overall surplus on world markets. A moratorium on this and

other new fisheries was put in place in 1991 pending development of criterion for controlled exploitation.

Alaska's fishery began recording *C. tanneri* as incidental catch in the developing trap fishery for Golden King crab (*Lithodes* aquespina) during the late 1970s . No directed fishery began until 1988 when special permits were issued by the Alaska Board of Fisheries for the deep water Tanner species *C. tanneri* and *C. angulatus* (ADF&G 1995). Two vessels received permits to fish the Bering Sea District. From 1989 to 1992, there was no directed effort and no market, however incidental catch was reported in the Golden King Crab fishery. In 1993, a size limit of 5" (127 mm) carapace width was established for permits from the Alaska Department of Fish and Game (ADF&G). Permits were for the Bering Sea and Eastern Aleutians Districts. By 1994, 100% observer coverage was required as the permit fishery developed to include the Western Aleutian and South Peninsula Districts with limited exploration permitted in the Chignik and Kodiak Districts. The fishery continued to develop with increasing landings and effort through 1995. In 1996 the Alaska Board of Fisheries instituted regulations stipulating trap size, type and configuration as well as escape mechanisms and trap limits for the South Peninsula and Kodiac Districts. This industry developed beginning in 1990 and recorded maximum landings in 1995 which declined in 1996 for several reasons. Fishing occurs year round and as yet does not have any seasonal or areal closures in place. Reported landings for 1993, 1994 and 1995 were 360, 580 and 1,270 tonnes respectively. Landings declined to 100,000 lbs. in 1996 and restrictions on harvest are in effect for the 1997 fishing season. (ADF&G news release Feb. 1997).

Some interest was expressed in developing of a *C. tanneri* fishery off Oregon during the late 1960s (Pereyra 1967) to harvest this untapped resource. Technological difficulties and economics largely prevented development of a fishery. However since the passage of a Developmental Fisheries Bill by the State of Oregon in 1993, a limited fishery has developed with reported landings of 140,000 lb. in 1996. This fishery is limited to 10 vessels at present and is not yet fully subscribed (Olson 1997, pers. com.). NMFS also conducts a limited annual trawl survey of the slope area from 550-1,160 m. The results of this survey are not available at present.

Management

The Alaska Department of Fish and Game (ADFG) manages Tanner stocks with reference to Alaska Board of Fisheries "Policy on King and Tanner Crab Resource Management "(90-04-FB, March 23, 1990). By this policy, the Department is required to establish a threshold level of abundance for each stock, data permitting. These data may include estimates of exploitable Biomass, estimates of recruitment, estimates of threshold level of abundance, estimates of acceptable biological catch, historical fishery performance data, estimates of reproductive potential, and market or other economic considerations (ADFG Commercial Shellfish Regulations 1996). Since data is limited, the Alaska fishery for *C. tanneri* is managed by size and sex (males only above 5") with area harvest limits set. Regulations stipulate that individual vessels require observer and logbook reports, and that restrictions *may* be placed on depth, seasons and areas

fished. Gear parameters and escape mechanisms are also defined in those regulations. Due to concerns about overharvest and discard mortality, area quotas in place for 1997 limit catch to a percentage of previous landings. Traps also require 2 escape rings of 4½" diameter (ADF&G News Release Feb. 1997).

REVIEW OF LITERATURE ON RELATED SPECIES AND DISCUSSION

For the shallow species. *C. opilio* and *C. bairdi* a great deal of information is available due to their circumpolar distribution, their commercial importance, relatively long establishment as fisheries and (in many cases) because of their shallow distributions in close proximity to research facilities. Elner (1995) comments "Arguably, Snow crab and its congeners have become the most studied crabs, second only to American lobster, in Brachyura, in scope of research effort". Some of what we do not understand regarding *C. tanneri* can therefore be surmised from the literature on these two congeners even though their habitat and behavior may differ substantially in other respects.

BIOLOGY AND LIFE HISTORY

Geographical and Bathymetric Distribution

General Distribution of the Genus Chionoecetes

The genus *Chionoecetes* has a circumpolar distribution (Jewett 1982, Slizkin 1989) and is comprised of 5 species. Two species, *C. opilio* and *C. bairdi* occupy relatively shallow water (< 400m) and are greyish to brown in color. Although *C. bairdi* is known from warm (10° C) water, this is basically a cold water genus. Of the two shallow water species, only *C. opilio* is found in both the North Atlantic and North Pacific oceans. The species ranges from the Gulf of Maine, along the eastern seaboard of Canada, the Gulf of St. Lawrence through to Greenland, and in the Pacific from Alaska through the Bering Sea to the sea of Okhotsk to the Japan Sea. There are no records of *C. opilio* from British Columbia.

C. bairdi, although known from as far south as Oregon (Hart 1982), occurs in abundance from northern British Columbia through the Aleutian chain to the Sea of Okhotsk and the Japan Sea. It supports a major commercial fishery in Alaska where it is known simply as Tanner crabs.

The other three species, *C. tanneri* (Grooved Tanner), *C. angulatus* (Angle Tanner) and *C. japonicus* (Zuwai crab) occupy relatively deep (cold) water. They are similar in size to their shallow water counterparts, *C. opilio* (Snow crab) and *C. bairdi*, (Tanner crab) but are immediately distinguishable by their bright orange coloration, enlarged branchial lobes of the carapace and slender walking legs. Only *C. bairdi*, *C. tanneri* and *C. angulatus* occur in British Columbia.

C. tanneri ranges from Mexico to the Bering Sea, *C. angulatus* from Oregon to the Sea of Okhotsk (Hart 1982), and *C. japonicus* is confined to the Sea of Japan in the western Pacific (Sinoda 1982). Off British Columbia, only the distributions of *C. tanneri* and *C. angulatus* overlap, although the latter is usually found in slightly deeper water (Hart 1982), the two species coexist throughout their geographic and bathymetric ranges. In the Bering Sea, their depth distributions were found not to be significantly different (Somerton and Donaldson 1996). It is expected that *C. angulatus* will constitute a portion of the bycatch throughout the range of *C. tanneri*, and therefore biological information on this species may also be collected during the course of fishery development. Although the deepwater Tanners are probably the most similar in terms of biological characteristics, relatively little is known of their biology and population dynamics due mostly to previous economic impediment to a deep water commercial fishery and to a lack of research activity.

Distribution of Chionoecetes tanneri *off British Columbia*

Jamieson (1990) hypothesizes a ribbon distribution along the continental slope bounded by the 550 m and 700 m contours. This narrow band, less than 5 km wide in most places constitutes the only known habitat off British Columbia (apart from isolated offshore seamounts). Although some mainland inlets have similar depths, no captures of this species have been reported.

The depth range of habitat critical to the population as a whole is probably 400 to 1,500 m to account for probable juvenile distribution (Pereyra 1967). It is not known what factors may influence their distribution although similarities in size of animals in catches between Oregon and Alaska (Somerton and Donaldson 1996) are suggestive of a very similar and uniform environment throughout their range. It would appear likely that *C. tanneri* is adapted to a fairly narrow range of environmental conditions, which apart from temperature and salinity, may further restrict local distributions within the preferred depth strata. Sediment composition and specific food requirement may be factors.

Juvenile distribution may influence adult distribution to some extent. For instance, Jamieson (1997, pers. com.) hypothesizes that *Cancer magister* distributions along the eastern shores of Vancouver Island may be limited by lack of suitable adjacent juvenile habitat; i.e. high temperatures or competition from an established species (Eggleston and Armstrong 1995) at a critical life stage (such as larval settlement), despite abundance of larvae for settlement and suitable adjacent adult habitat. There may also be gaps in juvenile distributions even though adult distributions appear contiguous, the available habitat being filled by migration of adults. Somerton and Donaldson (1996) note that juveniles in the Bering sea were found shallower than adults, the reverse of what is reported by Jamieson (1990) and Pereyra (1967). They conclude that this is probably due to local oceanographic conditions influencing larval transport and settlement. It is therefore possible that juvenile distributions may show considerable variability in depth along the British Columbia coast.

SEASONAL DISTRIBUTION AND MOVEMENT

Seasonal Migrations

As recorded by Jamieson (1990), adult male distribution off Vancouver Island is between 580 and 670 m, while females occur deeper between 670-720 m during most of the year. During late March to April however, females saturated traps in the same depth strata in which male crabs were caught previously. This phenomenon terminated the commercial fishery until the fall due to absence of large males in traps. Those that were caught had old, fouled carapaces. Clean shelled males and non-ovigerous females occurred in deeper water than was fished commercially. It would appear, then, that females moved shallower for the purpose of egg release and mating. Since no sampling was done between April and December, no reverse movement was documented. Spawning migration, if it occurs off Vancouver Island, is only over a distance of 2 km between average depths of males and females. These data, primarily from trap catches, may not reflect the true composition by sex due to agonistic interaction within traps (e.g. it is frequently observed in Dungeness crab fisheries, that large males may not enter traps already full of female or juvenile crabs). Seasonal data to document migration is lacking.

Pereyra (1967) found similar distributions off the Columbia River, Oregon from trawl data. There, major abundance of adult males occurred between 500 and 690 m while females occupied depths between 600 and 775 m. He describes a migration of males into deeper water for the purpose of breeding which he termed a spawning migration. This is the reverse of what was observed off British Columbia, where it appears that females migrate into shallower water. Movement began in the summer and took place over a 6 month period. The total horizontal distance covered was approximately 5 km giving an average daily rate of travel of 25 m.

Somerton and Donaldson (1996), found no significant difference in depth distribution between males and females and mean depth was also deeper (752 m for males, 709 m for females). These findings are based on only one cruise in late summer of 1982. Recent fishery information (Pengilly 1996) show females comprise a high proportion of commercial catches during the summer. Females sampled were found carrying batches of uneyed (recently extruded) eggs, and it is therefore unlikely that their association was for the purpose of reproduction at that stage. No migrations were apparent.

Segregation by sex and spawning migrations are well documented in the genus *Chionoecetes*. The reasons for segregation are not clear but may be the result of intraspecific competition (Somerton 1981; Sainte-Marie et al. 1995) as there is marked sexual dimorphism in all species. Alternately, segregation may be a response to microhabitat selection, crabs remaining aggregated by sex for protection or feeding. Somerton (1981) suggests (for *C. opilio* and *C. bairdi* in Alaska) that segregation occurs at time of maturity, the females remaining near the site where they matured while the males tending to undertake more random movement, perhaps directed during spawning

season by pheromones released by the females. Lovrich et al. (1995) observed that adult females tended to be more gregarious and sedentary than were the males. Pereyra (1966, 1968) also notes that female *C. tanneri* tended to be clumped whereas males tended to be more contagious in their distributions.

Breeding migrations from deep to shallow are documented for *C. opilio* (Ennis et al. 1990, Taylor et al. 1985, Hooper 1986) from Newfoundland and for the same species off Japan (Katoh et al. 1965). A possible explanation for migration into shallow (warmer) water is to increase the rate of embryonic development, and to ease the degree of thermal shock to larvae migrating from cold, deep water to warm surface waters for feeding and development (Taylor et al. 1985). This hypothesis cannot, however, explain migrations in deep-water species in which bottom temperatures vary less than 1° C over the entire distribution range (unpublished data courtesy of R.E. Thomson). Conan (1996) suggests that observed migration is actually the displacement of less fit crab as the result of competitive exclusion.

General Movement

No tagging studies have been conducted on deep water Tanner crabs. Tagged Snow crab movement has been found to be generally less than 20 km, with distances from point of tagging ranging from 0.6-74 km over periods of up to 5 years (Taylor 1992, Brethes et. al. 1989, Watson 1970, Watson and Wells 1972). Tagged *C. bairdi* off Alaska showed average movement of 24 km over 6 years (Donaldson 1980 Colgate 1982) with greater average displacements of 75 km reported by McBride (1982). Movement of other species of crabs, notably *Cancer magister*, tends to be local and generally random (Smith and Jamieson 1991; Diamond and Hankin 1985; Cotshall 1978). Although migration as a form of density regulation (Brethes 1989) cannot be discounted, it would appear from these observations that any movement of adult deep water Tanner crabs is likely to be random in nature and displacement is likely to be < 75 km over the adult lifespan.

REPRODUCTION

Overview

The reproductive process has been the focus of much of the research on Tanner crabs due to implications to harvest and management strategies. Crabs of this family (Majidae), typically undergo a terminal molt upon reaching reproductive maturity and cease to grow beyond that limit (Hartnol 1978). The presence of a terminal molt in *Chionoecetes* is generally accepted for females, but apart from *C. opilio* (Lovrich et al. 1995; Brethes et al. 1995), continues to be debated for males of the genus (Paul and Paul 1996). The absolute size at which terminal molt is attained often varies considerably within a species. The subject of reproduction is of critical importance to understanding the effect of male removal from a population (Paul and Paul, 1989). Our present knowledge of reproduction within the genus is briefly summarized below.

DEFINITION OF LIFE STAGES

Tanner crabs grow by a series of molts to adult (reproductive) size. It is important at this stage to adopt a standard for describing the various stages in sexual development. I will use those provided by Conan et al. (1989) in which crabs that show no gonadal development or morphometric differentiation are referred to as "immature", those with developed or developing gonads and with partial morphometric differentiation as "juvenile", and those with complete sexual development and morphometric differentiation as "morphometrically mature". A crab passes from immature to juvenile via a juvenile molt, and from juvenile to morphometrically mature via the puberal molt. Adult refers to a morphometrically mature crab that is in anecdysis (terminal molt). A further definition of "functionally mature" is sometimes applied to crabs which are of correct size and hardness to effectively mate with females in the natural condition (Conan and Comeau 1986, Paul and Paul, 1995), however since that definition is controversial and may be influenced by population dynamics, it will be avoided in this paper. These definitions continue to be debated in light of continuing research into the complexities of reproduction in the genus *Chionoecetes* (see Dawe et al. 1992 for the most recent review) and in Brachyura in general (Elner and Beninger 1992), however they will serve to outline possible reproductive pathways and strategies for *C. tanneri*.

Female Reproduction

The female crab copulates and extrudes fertilized eggs soon after the molt to morphometric maturity (Watson, 1972, Adams, 1985, Sainte-Marie and Carriere 1995). Even though gonads may mature in the juvenile state, reproduction for the female is impossible prior to morphometric maturity due to the requirement for widening of the third abdominal segment necessary for holding the extruded clutch of eggs during the incubation period. Thus for female crabs, the molt to maturity is the terminal molt and coincides with gonadal maturity. There is little evidence to suggest that mature female crabs undergo a further molt (Conan et al. 1990).

Females of both *C. opilio* and *C. bairdi* can be fertilized soon after terminal ecdysis while the shell is still soft, (primiparous females), or after subsequent release of the first or multiple batches of eggs during which the carapace is hard (multiparous females) (Adams and Paul 1983; Moriyasu and Conan 1988; Adams 1985). Additionally, spermatothecae allow storage of sperm not expended in spawning (Watson 1970; Adams and Paul 1983; Beninger et. al. 1988) and female crabs theoretically have the potential of fertilizing multiple batches of eggs after one breeding. Thus, female crabs are easily identified as either immature or mature and their breeding success is readily observed by the presence or absence of an viable egg clutch (it is possible for females to extrude non-viable eggs, Elner 1997 pers. com.).

Male Reproduction

Male crabs of *C. opilio* and *C. bairdi* can produce viable sperm in the juvenile state which is accompanied by first morphometric differentiation of the claw. (Conan et al.

1990). Successful breeding of primiparous females by juvenile (morphometrically immature) males has been demonstrated in the laboratory (Donaldson and Adams 1989; Moriyasu and Conan, 1988) but there is no documentation of this occurring in the wild. Males reach a second morphometric differentiation of the claw with the terminal molt. It is this stage that is generally thought to be responsible for most breeding. The equation of functional maturity and terminal molt has been questioned for *C. bairdi* (Paul and Paul 1995) since they demonstrated in the laboratory that small male, apparently morphometrically mature, crabs could continue to molt.

Copulatory behavior in adult Tanner crabs includes clasping and carrying of the female crab for extended periods prior to mating, often involving violent interactions with competitive males (Conan et al. 1990; Adams 1980, 1985, Donaldson and Adams 1989; Moriyasu and Conan 1988: Hooper 1986; Watson 1970). Large body size, in addition to fully differentiated chelae under these circumstances, are thought to provide selective advantage to successful breeding of multiparous females (Conan et al. 1990, Paul and Paul 1996; Stevens et al. 1993). Sainte-Marie et al. (1997) demonstrated that large body size was an advantage in both taking over a female from a rival and in defending a female from takeover by a rival. Additionally, in competitions between large males, the adult (terminally molted) crab was shown to have the advantage. Several other aspects of physical development and mating behavior also influence reproduction.

It has been observed that while in the new molt condition, primiparous females are flaccid and incapable of evasion and can be bred by males with smaller carapace widths (Donaldson and Adams 1989). Ennis et al. (1988) reported that in the absence of larger competing males, juvenile *C. opilio* could successfully mate with multiparous female crabs. However, these observations are from aquaria and their applicability in nature is uncertain.

Interactions

Stratification by depth and sexual maturity has been reported for *C. bairdi* (Donaldson et al. 1981, Stevens et. al. 1994), *C. opilio* (Sainte-Marie and Hazel 1992 Lovrich et al. 1995), *C. opilio* elongatus in the Sea of Japan (Kon 1968) and for *C. tanneri* (Pereyra 1966). Somerton (1982) suggested that breeding takes place between two distinct life history groups, one composed of primiparous females and recently morphometrically matured males, and the other between multiparous females and terminal molt males. He termed this segregated mode of reproduction "bipartite breeding". This hypothesis is supported (for *C. bairdi*) by submarine observation of mating aggregations (Stevens and Haaga, 1993) composed entirely of multiparous females which were being bred by a small number of large, hard shelled males on the periphery of the aggregation. Primiparous females, absent from the mating aggregation were widely dispersed in shallower water.

Moriyasu et al. (1987) and Moriyasu and Conan (1988) observed two types of mating behavior in *C. opilio*, one involving terminal molt, hard males and multiparous females, and the other between both juvenile and terminal molt males and primiparous females. Sainte-Marie and Hazel (1992) also report that terminally molted males were larger and

were found deeper in the presence of multiparous females, while smaller morphometrically mature males were found in shallow water in the presence of primiparous (newly molted) females. It would appear that "bipartite" mating is likely in other species of *Chionoecetes*.

Reproductive Potential

The reproductive potential of primiparous vs. multiparous females, and the viability of stored sperm for multiple fertilizations has also been examined. Paul and Paul (1992) found that wild *C. bairdi* could produce two egg clutches from one mating but viability of the second batch of eggs was low compared to crabs that bred annually. Furthermore, they found in laboratory experiments that primiparous females did not receive sufficient sperm after one breeding to fertilize a second batch of eggs in 10 out of 11 breedings. They also noted that over 90% of multiparous female *C. opilio* and *C. bairdi* captured at sea showed fresh grasping marks. This contradicts the previously held assumption (Hartnol 1978) that female Majid crabs required only one breeding to fertilize all the eggs produced in her lifetime. Paul and Paul (1992) suggest that this method of egg production may be auxiliary to fresh insemination. Other studies have shown that the presence of spermatotheca in multiparous females can have considerable regional and interannual variance (Beninger et al. 1988). Polyandry has been shown for *C. bairdi* (Donaldson and Adams 1989) and for *C. opilio* (Sainte-Marie et al. 1997).

Sainte-Marie and Lovrich (1994) estimated that *C. opilio* usually have enough sperm to fertilize at least one additional clutch of eggs. Sainte-Marie and Carriere (1995) therefore examined differences in reproductive potential of females using stored sperm and those bred a second time after release of the initial clutch. Their findings were that stored sperm produced similar viability to fresh sperm and further confirmed the observation (Adams and Paul 1983; Sainte-Marie and Lovrich 1994), that in Chionoecetes, volume of sperm stored after first spawning was unrelated to carapace width of the inseminating male. In a recent study (Saint-Marie et. al, 1997), volume of sperm in the spermatotheca was shown to be related to the time spent in copulation and further observed that large adult males copulated only once for a prolonged time, whereas juvenile males copulated numerous times but for only brief durations which may account for observed variability.

The contribution of primiparous vs. multiparous females to larval production for *C. opilio* was estimated to be >40% (Sainte-Marie 1993). It was observed that primiparous *C. bairdi* produced smaller numbers of eggs than multiparous females (Somerton and Meyers 1983) and it was suggested this was due to energy requirements of molting to adult and a smaller volume within the exoskeleton for ovarian tissue in the premolt condition. It was also observed (Sainte-Marie and Carriere 1995; Sainte-Marie et al. 1997) that females can apparently gauge the volume of their spermatheca and delay or interrupt spawning in hopes of securing another mate.

For *C. tanneri* it is not known whether males are capable of breeding multiparous females or whether they must be bred in the softshell condition. Somerton and Donaldson (1996) observed that 60% of new molt females were barren whereas

oldshell females without eggs amounted to only 16%. They suggest that molting in this deep-water species may not be as closely associated with breeding as is the case with shallower *C. bairdi* and *C. opilio*. No evidence confirms the ability to fertilize multiple batches of eggs, as has been demonstrated for shallow water congeners, although it is very likely. It is also not known whether a newly molted male crab will be able to mate in the same year. It has been demonstrated that it requires at least 90 days after molting before males can breed. This may be due to low levels of the hormone methyl-farinsoate, which has been shown to affect breeding activity in crabs. If the receptive period of female crabs is closely timed to an annual molting period, there may be insufficient time for newly molted males to harden and breed during that season. A fishery selecting for new shelled terminally molted males may remove them before they have had an opportunity to breed.

Summary of Reproduction

Reproduction in this genus appears to be a highly complex process which is only partially understood. Adult females can be bred in either the primiparous (soft) or multiparous(hard) condition and may segregate by depth and season. They may also fertilize a clutch of eggs from stored sperm which may further be influenced by physical and behavioral factors (see Elner and Beninger 1995 for review), which may favor last male precedence in fertilizing eggs (Paul and Paul 1996, Elner and Beninger 1992; Sainte-Marie and Sevigny 1996). Male mating behavior is sufficiently plastic to enable them to take advantage of any mating opportunity (Elner and Beninger 1995). They can mate either in morphometrically mature or morphometrically immature state with both primiparous and multiparous females. Sainte-Marie et al. (1997) have demonstrated a hierarchy in competitive breeding where large, hard shelled adult males are favoured.

EARLY LIFE HISTORY

Larval Period

Ovigerous females with late stage, eyed eggs were recorded in samples from late April off the west coast of Vancouver Island (Jamieson 1990). Observer data from Alaska (Pengilly 1996) show high percentages of late staged eyed larvae in March and April declining to near zero percent by June with a corresponding increase in new eggs. Planktonic feeding larvae are assumed for this species although inconclusively documented (Lough 1974). It was formerly thought that deep sea invertebrates, by reason of their depth and environment, produced only benthic larvae (Gage 1993). Somerton and Donaldson (1996) make the argument that egg volume in *C. tanneri* is insufficient for a lecithetrophic (non feeding) larva. A planktotrophic larva is more likely and may account for observed disparity of juvenile distributions between Oregon, B.C. and Alaska. Planktonic transport is alongshore or seaward off Oregon (Pereyra, 1967,) and shoreward in the Bering Sea (Somerton and Donaldson 1995).

Circumstantial evidence for surface larval transport is the presence of Tanner crab populations on isolated seamounts (Hughes 1981, Alton 1986). Pelagic larvae are

described for *C. opilio*, *C. bairdi* and *C. japonicus* (Sainte-Marie et al. 1995, Incze et al. 1987, Adams 1980, Haynes 1973;1977; Motoh 1978). It is highly likely that *C. tanneri* also produces a planktotrophic larva (Pereyra 1968) which is present in near surface waters for 2 to 4 months between April and August off our coast. Documentation of larval distribution remains to be done.

Larval period according to Pereyra (1967) and by observation of ovigerous females in our samples indicate larvae may be present near the surface from May through August off British Columbia. The oceanography of the slope region off the west coast of Canada from Juan de Fuca Strait to Cape St. James (southern tip Queen Charlotte Islands) is described by Freeland et al. (1984). Surface transport is predominantly northward during winter months due to the Davidson current, which generally relaxes during the period April through May. Surface transport is then southward during the summer months as a result of the California current. Transport of larvae should then theoretically be southward from point of origin. The behavior of the larvae, their depth distribution in near-surface waters and the degree of vertical migration is not known and will determine to a large extent, range of distribution. A larval period of 3-4 months is postulated based on observation of the time between egg release and subsequent recovery of newly settled crab (Pereyra 1966).

Bottom water temperature at 500 m varies between 3.7 and 5.7°C with an average temperature of 4.6°C; at 1,000 m it varies between 2.9 and 3.7°C with a yearly average of 3.36°C. Salinities average 34.08 ppm at 500 m and 34.38 ppm at 1,000 m. Current flow along the bottom is weak and often variable but predominantly northward. The source of the water mass is believed to be from as far south as California (Thomson 1997, pers. com., unpublished data). This is generally a very stable environment in terms of oceanography and annual variation in temperature and salinity.

Juvenile Distribution and Recruitment

Juvenile *C. tanneri* were found only in deep water off northern Oregon (Pereyra 1967). Recruitment to the adult population appears to take place from deeper water than the adult range. No juveniles were found in shallow habitats. Somerton and Donaldson (1996) found juvenile distributions in shallower water than the adults indicating that depth may not be the determining factor for successful settlement. The difference in distribution they accounted for by differences in local oceanographic conditions, i.e. direction of larval transport. An earlier survey of the Bering Sea (Tarverdieva and Zgurovsky 1985) also found them in shallower depths than adults.

Our observations (Jamieson et al. 1990) suggest juvenile distributions at depths greater than those of adults although incidental observations during sablefish surveys (Heritage pers. com.), suggest that small juveniles may be present over the depth ranges occupied by adult *C. tanneri*. There is no evidence for shallow water (< 400m) distribution of newly settled larvae off British Columbia and it is therefore assumed at present that juvenile recruitment (and settlement of larvae) occurs over the same depth range or in deeper water than adults. Pereyra (1966) describes an ontogenetic migration from deep water, but whether this represents an actual movement, or whether

it is possibly the result of cannibalism or predation on juveniles over the adult range requires more documentation. Juvenile distributions of the other deep water species are not well documented.

REPRODUCTIVE STRATEGY

If our assumptions about the larval history of *C. tanneri* are correct, then larvae are present in the plankton over a considerable time which would tend to favor dispersal over a broad area. Additionally, species fecundity appears high and reproductive capacity is further increased by ability of females to produce multiple batches of eggs in absence of recent fertilization. Such reproductive features would seem to compensate for variable reproductive opportunities and environmental conditions. Conan et al. (1990) concluded from a study of *C. opilio*, that environmental factors do not have random effects, but are naturally responded to in a population (of Tanner crabs). Compensatory mechanisms during reproduction, larval production, dispersal and settlement allow Tanner crabs to exploit any habitat opportunities which may occur.

Nizyaev and Fedoseev (1996) contrast reproductive strategies of King (lithodid) and Tanner species. The former tend to form mating aggregations, have external fertilization of eggs, require breeding for each batch of eggs produced, experience relatively high degree of egg loss during development, and undertake migration to juvenile habitat for egg release. Deepwater species also tend to have larger eggs producing a lecithotrophic (non-feeding) larvae. Juveniles tend to be habitat specific and the extent of juvenile rearing areas ultimately limits magnitude of recruitment to adult populations. Tanner crabs, on the other hand, have multiple reproductive strategies, have internal fertilization with the ability to store sperm for production of multiple egg clutches from one breeding and undertake only limited migrations prior to egg release and breeding. They experience relatively little egg loss through development, larvae can be widely distributed and tend to be robust in their ability to colonize different habitats.

Nizyaev and Fedoseev (1996) noted from their observations of Tanner populations in far eastern seas, that juveniles tend to form assemblages within areas of stationary gyres. They concluded that dispersal in the larval stage is not a mortality factor, and that success of recruitment in Tanners is related to early benthic predation, an observation made also by Lovrich et al. (1995) and Sainte-Marie et al. (1996) for *C. opilio* stocks, which will be discussed in more detail below. Predation on Tanner juveniles may be higher because they occupy fine grained bottoms with little natural cover. Young are not heavily armoured and tend to conceal themselves by burying in soft sediment. By contrast, they observe that major mortality in lithodid crabs takes place prior to settlement and during early benthic stages, before newly settled crabs can attain sufficient size and cover to become relatively immune to major predation. Lithodid crabs (and shallow water Tanners) have cryptic early benthic stages which occupy coarse bottom habitat offering concealment and protection, king crabs are heavily spined and are able to avoid most predation once they have attained a size of 25 mm (Nizyaev and Fedoseev 1996).

Distributions are also defined by reproductive strategy. Tanner crabs may join the reproductive process in any new marine environment, which they (Nizyaev and Fedoseev 1996) state, contributes to the permanent distribution of these crabs throughout the northern Pacific and also makes it impossible to define population boundaries except over large geographical areas. By contrast, lithodid species are confined to a defined rearing habitat. Migration of adults may enable the formation of colonies remote from these rearing areas with the result that these isolated colonies become functionally barren.

In conclusion, Nizyaev and Fedoseev (1996) state "...reproductive strategy is a complex of adaptive reactions, worked out in the course of evolutionary process to attain optimum conformity between reproductive processes and environmental conditions where any negative impact is compensated with proper alternative protective response".

STOCK DYNAMICS

Adult Population Structure

From the description of reproductive characteristics of Chionoecetes, it would appear that instability in adult population dynamics can be compensated for by the ability of the genus to produce large numbers of larvae per individual. This would suggest that population instability is inherent, and that a stock-recruitment relationship may not be apparent. This instability may be a function of the adult reproductive process or occur at a critical life stage. Some possible factors affecting the population dynamics of Tanner crabs are discussed.

There may be intrinsic fluctuations in adult crab populations, which may induce cyclic recruitment to that population in absence of any external factors. Two possible (and mutually exclusive) reproductive strategies involving physiological "choices" for males are postulated by Elner and Beninger (1995). The first scenario is one where immature males (MI) fail to copulate, i.e. are in an unfavorable climate due to competition from other males or avoidance by multiparous females. In this case, in which size and maturity confer a competitive advantage, a molt to maturity (MM) is triggered as it would increase their reproductive success. Implicit in this hypothesis is that MI males that bred successfully would continue growth in the immature state.

The second hypothesis is that successful mating by MI males would trigger a molt to MM status, whereas MI males that failed would opt for continued growth. The argument is that MI males are in a favorable reproductive environment and should not risk mortality through a series of growth molts, but should maximize their potential by quickly molting to MM.

A third hypothesis suggests genetic bias for small (under legal size) mature males as a result of intensive size selective fisheries (Elner and Beninger 1995, Jamieson et al. submitted). There is no evidence to date of this occurring, but the concept is being

examined in light of growing concern for efficacy of fishing regulations (Elner and Beninger 1995, Sainte-Marie 1993).

Elner and Beninger (1995) state that reproductive pathways should be viewed in the context of population dynamics, and as proportions of primiparous vs. multiparous females or mature vs. immature males changes either due to natural cycles in recruitment or through destabilizing fishing pressure resulting in a repeating pattern within fluctuating stocks. They characterize virgin stocks as "stagnant" where there is an accumulation of MM males and multiparous females. Observations reported by Conan and Comeau (1986) show that in a stable population, few immature individuals become morphometrically mature, requiring older individuals to disappear in order to make room for juveniles. Fishing may result in a "relic" population with insufficient large, MM male crabs to service the multiparous female population (Elner and Robichaud 1986, Beninger et al. 1988). Reduction of accumulated virgin biomass eventually allows a wave of recruitment which alters population structure in favor of IM males and primiparous females. As these crabs mature, the population approaches a climax phase where intrinsic growth rate slows. Without continued recruitment the population will ultimately return to the "stagnant" state (Elner and Beninger 1995).

Computer simulations by Mohn (1988) on an hypothetical crab population showed that density dependent mechanisms interacting with annual variance in reproduction could result in strong periodicity in abundance. Botsford (1986) suggests similar mechanisms may be responsible for observed ten year cycles of Dungeness crab (*Cancer magister*) off northern California. Recurrent (benthic juvenile) recruitment patterns are observed for *C. opilio* in the Gulf of St. Lawrence (Sainte-Marie et al. 1996) with five moderate to strong year-classes alternating with three consecutive weak year-classes. Other fisheries for *C. opilio* and *C. bairdi* undergo apparently natural fluctuations which are probably influenced or possibly driven by the complex interactions surrounding growth and breeding. Due to this complex relationship, detailed knowledge of population composition is prerequisite to understanding stock dynamics or predicting potential fishing effects.

Recruitment Patterns and Population Fluctuations

An isolated and little fished Snow crab population was observed over a 10 year period (Comeau et al. 1991) in Bonne Bay, Newfoundland. There, fluctuations in the population could be observed independently from fishing effects. Factors such as egg production, ice cover, and oxygen depletion could not be demonstrated to affect recruitment. Juveniles showed wide tolerance to bottom type, avoiding only boulder areas. Survival was best where protection from cannibalism and predators was best . They felt natural fluctuations in the population (confirmed by fishermen) was the result of intra-specific competition. The suggested mechanism was cannibalism by terminal molters on juvenile and immature crabs. This would produce waves of recruitment as the dominant cohort died of old age leaving room for a wave of new recruits which would, over several years, again dominate the system. They speculated that such waves were a mechanism to avoid predators targeting them as a sustaining food source.

A commercially exploited population of *C. opilio* was examined by Sainte-Marie et al. (1996) in the Gulf of St. Lawrence. They observed an alternation of strong and weak year-classes that repeated over a period of approximately 8 years. Year-class strength was determined early suggesting that settlement intensity or early survival were critical agents in determining strength of the year-class. They also concluded that the cause was endogenous through a similar mechanism of negative, density dependent interaction with preceding age groups. Fernandez et al. (1993) record similar repression of developing year-classes in Dungeness crabs. The establishment of such cycles causes periodic shifts in adult population structure which is reflected in the fishery by periodic shifts in maturity and size composition of legal males.

A recent study (Lovrich et al. 1995) of Snow crabs from the northern Gulf of St. Lawrence also concluded year-class strength was determined at time of larval settlement or shortly thereafter, and that an endogenous mechanism(s) was primarily responsible for observed recurrent fluctuations in the fishery of 3 weak year-classes followed by 5 strong year-classes. They proposed three hypotheses that might explain observed variation. The first, larval production, was based on the observation that weak year-classes in the adult population tended to produce less larvae. The second, competition during early benthic stages for a limited habitat is similar to that of Sainte-Marie et al. above. The third hypothesis is that adult crabs periodically inhabit the same habitat as juveniles (i.e. during winter breeding migration). In years of high adult abundance, it is suggested that adults impede juvenile year-classes either through cannibalism or direct competition. Although temperature was suggested as being a critical factor in juvenile survival, the recurrent weak and strong year-classes could not be explained by this variable in relation to juvenile habitat.

Cycles have also been observed for *C. opilio* in the sea of Japan (Kon et al. 1993) and for *C. bairdi* (Colgate1982). It would appear from these observations that fluctuations in abundance of *C. tanneri* may be a natural occurrence and may be due to endogenous mechanisms rather than mainly environmental ones. The presence of cycles in adult biomass and age structure for this species should not be surprising.

GROWTH AND AGE

Age at Maturity and Lifespan

Crabs grow by molting their exoskeletons. As a result, there are no hard structures with which to estimate the total age of the crab. Approximation of age by identifying modes in population frequency distributions works well only for the early development stages as modal frequencies are masked by sexual and regional differences in growth rates as crabs mature. Nevertheless, this technique has been used to estimate the age structure of several species of Chionoecetes.

An early model by Watson (1969) for *C. opilio* based on CW frequencies of juveniles and values from the literature for larger crabs estimated growth to legal size of 95 mm CW, occurred at instar XIII and took 9.5 years. Robichaud et al. (1989), using trawl data

for *C. opilio*, collected in the southeastern Gulf of St. Lawrence, inferred number of instars, molting frequency and molt increment from CW distributions. They concluded that males reached the legal size at instar XI or within 4.5 years after hatching. However , development of an accurate growth model was compromised by lack of good information on molt periods and growth per molt which incorporated changes in growth related to maturity. Sainte-Marie et al. (1995) produced a model which took into account not only observed modal frequencies in fishery and trawl samples, but gonadal development, chela allometry, and molt increments measured in the field and laboratory. They found that molting became annual after Instar VI until near morphometric maturity when intermolt periods of 24-27 months were possible. The minimum age at which a crab could attain legal size was estimated to be 8.7 years however, allowing time for the shell to harden after that molt, the practical age at which the crab would become commercially valuable was approximately 9.5 years. Observations of year-classes entering the fishery (Sainte-Marie et al. 1996) give the time interval from hatching to impact on the fishery of about a decade. At present it is estimated that morphometrically mature males do not survive more than 5-6 years after terminal molt (Comeau et al. 1991, Sainte-Marie et al. 1995) or 5 years for females (Mallet et al. 1993) which would produce a maximum lifespan of 13-15 years for males and at least 10-12 years for females due to their earlier entry into the terminal molt.

Kon et al. (1968) record 9 instar stages to reach maturity for males and 10 for female *C. opilio* in the Japan Sea, however no ages were assigned. A growth curve was constructed for Alaskan *C. bairdi* (Donaldson et al. 1981) based on observed CW frequencies in fishery samples and from survey data. Their estimate of growth to 50% maturity was approximately 6-7 years at Instar XIV, and estimate of 8.8 years (Instar XVI-XVII) to entry into the fishery. They give a maximum age of about 10 years, but caution that skip molting may produce greater ages than those calculated. Somerton (1981) by observation of a dominant year-class moving through a fishery, suggested that female *C. bairdi* may live up to 7 years after terminal molt.

No approximation of age at maturity has been attempted for the other (deepwater) species although Tester and Carey (1986) traced the development of *C. tanneri* through 7 instar stages requiring approximately 20 months from hatching to attain a size of 26.8 mm. Growth increment between molts may be relatively constant due to the uniform environmental conditions at depth. They also remarked on the similarity in size between similar instars taken from their study site off northern Oregon and samples from the Farallone Islands off San Francisco, California. Similar uniformity might be expected off our coast in terms of growth rates, size and age at maturity and maximum age. Somerton and Donaldson (1996) noted the marked similarity of size at maturity between Alaska and Oregon for this species contrasted to marked differences observed for *C. bairdi* and *C. opilio* over a distance of 200 km (Somerton 1981).

Molt Cycle and Intermolt Duration

Of major importance to understanding population dynamics of *Chionoecetes* is the molt cycle, frequency of molting and the duration of the intermolt period, especially as it

pertains to physiological maturity and terminal molt. Problems arise in determining the time elapsed since the last molt due to any absolute measure of shell age.

Determining the position in the sequence of molt events by examination of mouthparts has been fairly well documented for *C. opilio* (Moriyasu and Mallet 1986, O'Halleran and O'Dor 1988) The outward appearance of the shell (color) and formation of a new carapace underlying the old one in crabs about to molt has been correlated to stages determined from mouthparts (Hoenig et al. 1994). However, field estimation of shell age based on outward signs of shell abrasion and epifaunal growth are subjective and to some degree dependent on experience of the observer.

Various shell age (hardness) scales have been developed (Miller and O'Keefe 1981, Somerton 1982, N.M.F.S. 1993, Hoenig et al. 1994, Somerton and Donaldson 1996) which have been verified to some extent by tag returns, physiological examination of underlying new shell development, and laboratory observation. Problems arise in assigning an absolute age to mature crabs judged to be old shell. Preliminary observations using radiometric methods comparing ratios of $^{228}TH/^{228}Ra$ (Nevissi et al. 1996) indicate shell ages of 4-7 years for some of these. This agrees favorably with estimates for life span after terminal molt above. Donaldson et al. (1981) from results of tagging, record intermolt periods exceeding 3.7 years.

Shell condition (age) codes developed for shallow water species may not be directly applicable to deepwater species. Encrusting organisms may require longer to establish, or reduced activity levels or different foraging or mating behaviors may retard shell abrasion. Tag studies or radiometric shell aging techniques may be required to verify ages unless clearly dominant year-classes can be observed in a fishery. Both Tester and Carey (1986) and Somerton and Donaldson (1996) noted that a greater percentage of female crabs had old, fouled and abraded carapaces than did males. Sex ratios in favor of females were observed by Pereyra (1966), Tester and Carey (1986) and Somerton and Donaldson (1996). Tester and Carey (1986) suggested (based on an earlier suggestion by Barros et al. 1978), that males molt frequently enough as adults to keep their carapaces free of fouling. This, as well as the unbalanced sex ratio which they suggested was mortality associated with more frequent molting, were cited as evidence for continued molting in males past morphometric maturity. Somerton and Donaldson however do not consider the low proportion of old shelled males and higher proportion of females in their samples is conclusive of the absence of a terminal molt for *C. tanneri*. They suggest that these observations may be accounted for by differences in sampling time, habitat or differential mortality rates from other causes. Jamieson et al. (1990) reviewed the issue and also concluded that observations presented may have been sampling artifacts.

Shell age may be an important factor in breeding success of large males. A study by Paul et al. (1996) showed that in competitions between crabs of similar size, old shelled crabs outcompeted new shells in over 70% of the trials. Underestimation of shell age, undiagnosed disease, damage to the exoskeleton and senility are proposed as possible factors in those trials where new shelled individuals won. Shell age may become

important in a fishery that harvests only large, hard shelled individuals. Taylor et al. (1989) report shell hardening after a molt in *C. opilio* to be complete within 90 days. Paul and Paul (1995) found that breeding does not take place (in *C. bairdi*) for at least 99 days after molting. There is evidence from other Majid species (Sagi et al. 1994) that mating is inhibited for a period after molting and that new shelled crabs may not breed regardless of their shell hardness. If there is an annual spawning season (Pereyra 1966, Jamieson 1990, Pengilly 1996, unpublished) coinciding with egg release and molting as has been suggested by Pereyra (1966), then a recently molted male may not be able to participate in mating during that year. Accurate shell age would be important in estimating what portion of the male population was available for breeding.

PHYSIOLOGY, FOOD AND FEEDING

Deep Sea Adaptations

C. tanneri exhibit a number of adaptations commonly associated with bathyal crustaceans (Somerton 1981, Barros et al. 1978, Childress 1971 a,b, Takeshita 1978). These include enlarged branchial chambers and gills, red coloration and elongated limbs in comparison to shallow water congeners (Somerton 1981). The enlarged branchial chambers house enlarged gills which serve to enable the crab to survive in low oxygen (7% of surface values or 0.5ml/l) environment typical of the depth strata occupied by this species (Favorite et al. 1971). This adaptation is noted in other crustacea normally confined to oxygen minimum zones (Childress 1971a). Branchial chamber enlargement compared to shallow water *Chionoecetes* are shown by moiré photography and cross sectional profiles (Takeshita 1978), and is comparable to deepwater lithodid crabs which show similar branchial enlargement. The red coloration is generally considered an adaptation of deep dwelling crustaceans to avoid visual predation as red light from the surface is attenuated rapidly with depth and is produced only at low levels through bioluminescence (Marshal 1954). The elongated legs and reduced musculature are probably a means of conserving walking energy in a low energy environment (Childless, 1971b). Meat yield (muscle tissue) is reported less for *C. tanneri* than for shallow species (Jamieson et al.1990; Tri-Star processors, pers. com.).

These physiological adaptations suggest a marginal environment. Metabolic and growth rates may be lower than in shallow species which would influence the degree of fishing impact. Lower oxygen consumption for deep living species has been demonstrated by Childress (1971b), which would indicate an overall lower metabolism. A number of authors have examined metabolism of *C. opilio* (McLeese and Watson 1968, Foyle et al. 1989, Thompson and Hawryluk 1989) and *C. bairdi* (Paul and Fuji 1989) over the range of ambient temperatures found in the fishery. A negative energy balance was demonstrated in some cases due to low temperatures, however *C. tanneri* does not experience temperatures below 4° C throughout its range (Pereyra 1966, Thomson 1997 pers. comm.) and low temperature is therefore not as likely to influence metabolic rate in this species as are oxygen levels and food uptake. However, Gage (1993) remarks "that the prediction of the deep sea as a non-seasonal environment supporting

a low activity ecosystem, with its component populations showing unusually slow rates of recruitment and growth and an age structure dominated by old individuals, has no universal validity". This may be especially true of a population inhabiting the slope of a highly productive continental shelf with demonstrated upwelling occurring near the shelf break (Thomson 1981).

Food and Feeding

One study has been done for *C. tanneri* from the Bering Sea by Tarverdieva and Zgurovski (1985) in which they describe the diet of several deepwater crabs including that of *C. tanneri*. Large (adult) crab stomachs contained fish, ophiuroids, decapods, mollusks and polychaetes; small (juvenile) crabs contained mostly ophiuroids and polychaetes while immature crab stomachs contained polychaetes, amphipods and ophiuroids. There was some variation in diet between areas with a tendency for larger crab to feed on a wider spectrum of food items. A photograph (Hughes 1981) shows individual *C. tanneri* feeding on mud dwelling organisms at 689 m on Giacomini Seamount in the Gulf of Alaska.

There have been numerous studies on the diets of the shallow water species. *C. opilio* and *C. bairdi* (Yasuda 1967, Tarverdieva 1976, Paul et al. 1979, Miller and O'Keefe, 1981, Jewett et al. 1982), which show marked similarities in food items over their range. Of note is the reliance on polychaetes, bivalves and various crustacea. Larger crabs feed on ophiuroids and fishes to a greater extent (Jewett 1982), perhaps because they are physically able to do so. Lefebvre and Brethes (1990) report that young of *C. opilio* fed predominantly on polychaetes, followed by small crustaceans and mollusks. The range of food available to shallow water Tanners is probably greater due to the diversity in habitat, especially between adults and immature crabs.

Tanner crabs held in the laboratory have been observed to eat a wide variety of food from fish food pellets to chopped herring and dead shrimp (personal observation). Small *C. bairdi* (50 mm CW) readily consumed large (20 mm test diameter) brittle stars. Tanner crabs in the wild are undoubtedly opportunistic feeders (Tarverdieva and Zgurovski 1985, Jewett 1982) and dependence on the rain of detritus and corpses of fish and other pelagic species increases for bathyal inhabitants (Young and Eckelbarger 1993).

Below the photic zone, all marine life is supported by nutrients supplied from the surface in one form or another, or from production occurring near hydrothermal vents (Tunnicliffe 1991). An estimated 1% of the surface production reaches abyssal depths (Gage and Tyler 1991) which fuels the benthic ecosystem. In this environment it would clearly be an advantage to detect, at a distance, carrion or other such material. Observations were made on *C. tanneri* held in aquaria. The response to dropping food into an aquarium was nearly instantaneous as the crab began to "locate" the food source by a series of body rotations followed by short "tacks" which served to resolve the direction of the food. Such behavior probably serves to locate windfall food sources in the wild. Once the Tanners had eaten for several hours, they showed no further interest in the food for a period of days however.

Somerton and Donaldson (1996) have suggested that pheromones serve to bring crabs together for breeding, suggesting that their chemical detection ability is acute. The range over which a crab can detect food is perhaps of consequence as it applies to trap performance and CPUE. Crabs may be attracted over considerable distances, especially with long soak times, which may serve to keep observed catch per trap artificially high with an abrupt decline as crab stocks are exhausted.

SOURCES OF MORTALITY

Predation

Tanner crabs are probably prey for all the larger fish and invertebrates. No specific studies have been done on *C. tanneri*, however crabs of the genus *Chionoecetes* are one of the most commonly taken benthic prey in the northern Pacific Ocean (Jewett 1982). The genus is probably second only to pandalid shrimps in receiving predation pressure due to their great abundance and dominance of the benthic habitat (Jewett and Feder 1982). *C. opilio* can, at times, comprise as much as 35%-50% of the invertebrate biomass (Lovrich et al. 1995). Feeding studies (*C. opilio* and *C. bairdi*) conducted throughout their range indicate at least twenty-six species of fish, seven invertebrates and four marine mammals commonly eat the adults. Early benthic larvae are consumed by fish (Tester and Carey 1972) and are very likely cannibalized over the adult range. As mentioned above, *Chionoecetes* lack the heavily spined carapace of Lithodid crabs and bury in the substrate to avoid predation (Nizyaev and Fedoseev 1996). Aggregative behavior has been observed in *C. bairdi* (Stevens et al. 1994) which, although probably a breeding adaptation, also functions to reduce predation.

Predation on *C. tanneri* is of relevance to the recruitment of benthic juveniles to the adult population. Heavy predation at a particular juvenile life stage may prevent that year-class from establishing. This may account for holes in their distribution or be a factor in intrinsic population fluctuations. Predation upon discards may also be of importance. The fishing depth (500-1000 m) means that crabs discarded at the surface would take considerable time to reach the bottom. Predation may then occur in midwater regions as well as on the bottom. Crabs that do reach the bottom may be stressed due to handling effects or temperature and pressure change and may be particularly vulnerable to predation. Gooding (1985) observed increased mortality in uninjured lobsters released from pots primarily from disorientation caused by falling through the water column. This aspect will be discussed further below. We have personal observation of discarded Dungeness crabs being captured and eaten by the sunflower star (Pycnopodia spp.) due to the crab's lethargic and disoriented condition upon reaching the bottom. Crabs would normally show an immediate flight response.

Handling Mortality

Mortality associated with capture and handling has been a concern for investigators for trap caught crabs (see Murphy and Kruse 1995 for review). Injury and death due to

handling, is frequently observed with newly molted (soft) crabs but the cumulative effects of physiological stress and sublethal injury are difficult to assess. Handling injury could result in infection by chitin dissolving bacteria (Baross et al. 1978) which are bioluminescent and may predispose the crab to predation. Aggravated injury may reduce the crabs ability to compete during breeding (Paul and Paul 1995, Paul and Paul 1996). Injured limbs are readily automotized by crabs (Miller and Watson, 1976, MacIntosh et al. 1996), however the implications of such injuries, especially if they occur to a terminally molted crab, are not clearly understood. Various experiments have been conducted where handling effects have been simulated. MacIntosh et al. (1996) evaluated separately, the effects of dropping on deck, dropping from deck height into water, induced carapace and limb injuries and repeated handling. They concluded after a 60 day holding period that there was no difference between the treatment and the control groups. A similar study of the handling effects on King crabs (Zhou and Shirley 1996) also failed to show significant mortality due to handling effects but noted that predation on discarded crabs was a possibility. Effect of handling could be delayed until time of molt which would then become apparent as differential mortality rates for injured crabs.

Another source of mortality which has been little investigated is the effect of displacement on discards. A crab discarded 1,000 m above the bottom may be carried a considerable distance by currents etc. before landing on bottom. Alternately, the fishing vessel may drift resulting in the crab being displaced from its normal habitat, either deeper or shallower. The effect of such displacement may be increased predation or an inhospitable habitat in terms of food or competition. Discarded Tanner crabs contain air under their carapaces and failure to adequately "burp" them may result in them floating for an unknown time in warmer surface waters. The effect of thermal stress has been studied for other species (McLeese 1968), but is unknown and would be dependent on the time of year. Jamieson (1990) suggests that temperature may have been a major mortality factor in summertime around the seamounts sampled due to the high (14°C) oceanic surface water.

Discard mortality was thought to contribute to the collapse of the King crab fishery in the Gulf of Alaska (Kruse 1996), and is a concern for the present fishery there for *C. tanneri* (ADF&G News Release Feb. 1997). For the Tanner fishery off Dutch Harbor during 1994, it was estimated that 1 female or undersized male was released for every legal crab harvested (Tracy 1995). Handling mortality of sublegal crabs is thought to represent a considerable economic loss to the fishery for Dungeness crabs in B.C. and the magnitude of this loss is currently under investigation. The handling of discards should be duly considered in developing a new fishery for *C. tanneri*.

Diseases and Parasites

At least 3 major pathogens have been identified in Chionoecetes.

Bitter Crab Disease

Bitter crab disease was first discovered in 1985 in *C. opilio* and *C. bairdi* from Alaska (Meyers et al. 1990). It imparts a bitter taste to crab meat rendering it unusable. The disease is caused by a dinoflagelate parasite (*Hematodinium spp.*) in the hemolymph which produces a wasting disease ultimately resulting in death of the host (Love et al. 1993). The disease is present in approximately 1/3 of the commercially fished areas of Alaska, and infestation rates as high as 90% have been recorded in some areas (Meyers et al. 1990, Love et al. 1993). Discard rates have averaged about 4% since 1989, representing a significant loss in landed value.

External indications of the parasite include a pinkish abdomen and carapace, white lines along the underside of each leg and milky hemolymph. Lightly infected individuals are apparently indistinguishable from uninfected in taste. Tanner crab condition does not appear to be compromised until the latter stages of the disease during which dinospores are released and the crab becomes moribund and dies. In *C. bairdi*, this occurs during late summer or fall, thus allowing infected individuals to complete egg incubation. Effects of long term parasitism on host growth rates have not been done (Love et al. 1996).

Similar dinoflagelates are known to infect a wide range of crustaceans (MacLean and Ruddell 1978) including the blue crab *Calinectes sapidus* (Newman and Johnson 1985, Couch and Martin 1979), the Norway lobster, Australian Portunid crabs, and at least two species of Xanthid crabs (Field et al. 1992, Shields 1992, Hudson et al. 1993) in addition to *C. bairdi* and *C. opilio*. A similar parasite infects spot prawns (*Pandalus platycyros*) and pink shrimp (*Pandalus borealis*) from British Columbia. and Alaska (Bower and Boutillier 1993, Meyers et al. 1994). Although there are no reports of this parasite infecting *C. tanneri*, there is reason to believe infection is possible.

Black Mat Disease

Black mat disease is an encrusting fungus infection caused by the ascomycete *Trichomaris invadens* (Hibbits et al. 1981). The fungus forms a thick tar-like mass on infected individuals from which the name is derived, but also invades the cuticle and various deeper tissues and may prevent molting and eventually causes the death of the host (Sparks 1982a). The effect on growth rates and implications of the disease preventing molting have not been investigated but mortality associated with this disease may have been partly responsible for the decline of *C. bairdi* stocks in the 1980's (Sparks 1982b). The disease occurs primarily on *C. bairdi* in Alaska but is known to occur on *C. opilio* and *C. tanneri* (Hicks 1982). We have no reports on infected individuals from B.C.

Nemertean Egg Predators

Nemertean worms infect a number of commercially important crustaceans (Wickham, 1986), and are known to cause egg loss in Red King crabs and Tanner crab species from Alaska (Shields et al. 1990) and in Dungeness crabs (Wickham 1979). These worms show low host specificity, which may contribute to their survival (Wickham and Kuris 1990). It is possible they can also infect *C. tanneri,* although infestation has not

been reported. Wickham and Kuris (1990) suggest that infection of *C. bairdi* may be high enough to seriously affect brood strength, although the role in population dynamics has not been investigated. Shields et al. (1990) consider these worms a major source of egg mortality in certain Red King crab stocks, to the extent that they may conceivably cause recruitment failure.

HABITAT, ECOLOGICAL AND ENVIRONMENTAL RELATIONSHIPS

Overview

C. tanneri occupy the continental slope region which has until recently been below the depths of benthic commercial fisheries. It is the dominant large invertebrate in that environment. Only *C. angulatus* overlaps its distribution. These two species may occupy an extreme environment in relation to other members of the genus and other crabs in general which have shallower distributions. Bottom type is predominantly fine sediment supporting a variety of invertebrates which feed on detritus from the photic zone above. Tanner crabs occupy a niche as predator/scavenger, feeding for the most part on worms, small crustaceans and mollusks, but are also opportunistic feeders on larger pieces of carrion (Tarverdieva and Zgurovski 1985).

Faunal Associations

Pereyra (1967) identified fauna associated with *C. tanneri* as belonging to a mid depth assemblage. This is in part due to the wide bathymetric range of the samples. However, if the assemblage is restricted to only those tows in which 6 of 8 species occurring in a group are recurrent, then the assemblage is more closely associated with deep water groups. Species commonly associated with *C. tanneri* off the mouth of the Columbia river include:

(affinities greater than 0.5 in decreasing occurrence from Pereyra 1967)

Species	**Common name**
Neptunea amianta	Neptuneid whelk
Heterozonius alternatus	Astroid
Antimora rostrata	Longfinned cod
Careproctus melanurus	Pink liparid
Apristurus brunneus	Brown cat shark
Thrissacanthius penicillatus	Asteroid
Albatrossia pectoralis	Pectoral grenadier*
Sebastolobus altevelis	Longspine thornyhead *
Sebastolobus alascanus	Shortspine thornyhead*
Solaster borealis	Asteroid
Anoplopoma fimbria	Sablefish
Coryphaenoides acrolepis	Ratail grenadier

Species	Common name
Nearchaster acilulosis	Asteroid
Bathybembix bairdi	Gastropod
Microstomus pacificus	Dover sole
Zoroaster mordax	Asteroid

* Fish species names are according to Gillespie (1993) for continuity. They are changed from the original.

It can be expected that some of these species will also form part of the assemblage off British Columbia. Species known to occur as either bycatch in the limited fishery for *C. tanneri* and the research cruise in 1988, or from species associated with sablefish trapping (Smith et al. 1996) include (no abundance order implied):

Species	Common name
Roundfish	
Albatrossia pectoralis	Pectoral rattail
Antomora microlepis	Longfinned cod
Careproctus melanurus	Blacktail snailfish
Coryphaenoides acrolepis	Rougheye rattail
Gadus macrocephalus	Pacific cod
Icosteus aenigmaticus	Ragfish
Macrouridae sp.	Rattail sp.
Microstomus pacificus	Dover sole
Rockfish	
Sebastes aleutianus	Rougheye rockfish
Sebastes borealis	Shortraker rockfish
Sebastolobus alascanus	Shortspine thornyhead
Flatfish	
Atherestes stomias	Arrowtooth flounder
Embassichthys bathybius	Deepsea sole
Eopsetta exilis	Rock sole
Errex zachirus	Rex sole
Hippoglossoides stenolepis	Pacific halibut
Pleuronectes vetulus	English sole
Selachi	
Apisturus brunneus	Brown cat shark
Somniosus pacificus	Pacific sleeper shark
Squalus acanthius	Pacific dogfish

Species	Common name
Invertebrates	
Asteroidea sp.	Asteroids
Chionoecetes angulatus	Angle tanner
Chionoecetes bairdi	Brown Tanner
Fusitriton sp.	Whelks
Lithodes aequispina	Brown king crab
Lithodes couesi	Queen crab
Lopholithodes foraminatus	Box crab
Octopus sp.	Octopus
Ophiuridae sp.	Brittle stars

Environmental conditions

The deep environment occupied by *C. tanneri* is marked by low annual fluctuations in temperature, salinity and oxygen, nearly perpetual darkness and uniform bottom type. Sedimentation rates and current velocities are generally quite low and deepwater inhabitants tend to be slower growing and older than similar shallow water taxa (Gage 1991). Most activity is confined to the first several cm. of the bottom and the environment in general may be more fragile. Hastie (1995) remarks on a fishery for deepwater crabs "given the deepwater distribution at low temperatures, slow growth and maturation rates and possible infrequent recruitment of Geryonid crabs, it is doubtful that high yields are sustainable." Nevertheless, the deep sea benthos can be surprisingly diverse and dynamic showing marked seasonality (Young and Eckelbarger 1994). Overall productivity may be greater than originally assumed.

Fishing Infringement

At present, only the sablefish (*Anoplopoma fimbria*) trap fishery impacts the upper depth distribution of *C. tanneri*. This is a highly selective fishery using gear in which Tanner crabs occasionally appear as bycatch. A developing trawl fishery for slope rockfish species may overlap Tanner habitat. The implications of such a non selective fishery are not discussed here, but trawling may have adverse effects on bottom habitat, and is almost certain to cause a degree of crab mortality (Solving Bycatch 1996).

SUMMARY OF BIOLOGICAL INFORMATION

1. Deepwater Tanner crab (*C. tanneri*) are found on the continental slope between approximately 500-1,000 m. Juveniles are probably deeper than adults in the south, however nothing is known of their relative distributions north of Vancouver Island. Sexes appear to be segregated during most of the year.

2. Reproduction appears to take place on an annual cycle, however that does not discount the possibility of longer cycles. Larval release, molting , breeding and egg extrusion appear to take place during late spring off B.C. The precise sequence and timing of events is unknown.

3. A terminal molt is assumed for *C. tanneri*. It is possible that large clawed males can continue to molt, however there is no evidence to suggest that females molt past sexual maturity. Life span after terminal molt is probably less than 7 years. Total lifespan is probably less than 15 years.

4. Several reproductive strategies are possible in *C. tanneri*. Females can probably be bred in the newly molted softshell (primiparous) or in the hard shelled (multiparous) states and may also be able to fertilize eggs using stored sperm. Males can likely reproduce as morphometrically mature adults or as juveniles depending on population structure. However, in terms of risk averse management, it should be assumed that only primiparous females breed with terminally molted (adult) males.

5. A planktotrophic larval stage is assumed for this species. Larval release is probably timed to the spring plankton bloom. Larvae must then undergo an extensive (>600 m) vertical migrate to near-surface waters where feeding likely occurs. This implies the potential for considerable dispersal depending on degree of vertical migration exhibited by the larvae and the depth strata occupied. Residence time in the plankton is estimated to be of 3-4 months. Settlement, or at least recruitment of benthic juveniles appears to occur from deeper than the adult depth range. It is possible that juveniles could be found shallower in some areas of the coast.

6. The environmental conditions at depth are relatively uniform. Growth rates and size at maturity probably reflect that uniformity.

7. Bottom type preferred by this species appears to be fine sediment. Food likely consists of polychaetes, mollusks, benthic crustaceans, ophiuroids and fish. They are also opportunistic feeders on larger particles from the surface and can probably locate such food at a distance.

8. *C. tanneri* is probably food for all of the larger fishes and invertebrates found in their habitat. Adult crabs are probably cannibalistic on juvenile and immature crabs, especially in the newly molted state.

9. Crab species that share the range with *C. tanneri* include *Lithodes aequispina*, *Lithodes couisi* and *C. angulatus*.

10. *C. tanneri* populations probably experience naturally occurring fluctuations and these may be cyclic.

11. *C. tanneri* are probably subject to several diseases or parasites infecting other species of Chionoecetes. These include a dinoflagellate blood parasite, an invasive fungus disease and a nemertean egg-eating worm.

A summary of biological knowledge is presented in Table 1

Table 1: Tanner Crab Life Table

Common name	Tanner crab (B.C.) Grooved Tanner (Alaska) Deepwater Tanner	Snow Crab (N.A.)	Tanner Crab (Alaska) Zuwai Crab (Japan)
Scientific name	*Chionoecetes tanneri*	*Chionoecetes opilio*	*Chionoecetes bairdi*
Geographic range	Alaska - Mexico	circumboreal. Atlantic; Newfoundland Gulf of St. Lawrence Pacific; Gulf of Alaska Does not occur in B.C.	Pacific only; Alaska- Oregon Aleutians Sea of Japan Othotsk sea
Depth	458 -1784 (Hart, 82)	0-310m (Elner 1985)	0-200m (Hart 1982)
Male (Fishing)Depth	500-550m off Or. (Pereyra 68)	75-300m (Miller and O'Keef 1981	50-160m (Stevens and MacIntosh 1989)
Maximum size (mm)	181mm CW	150mm (Powles 1968)	200mm (Donaldson et al.1981)
Maximum age	<15 yr (est)	5yr past term. molt (Mallet 93) 13-15 yr	10-12 Yrs (Donaldson et al.1981)
Legal size	ND 110mm (market)	78mm (Alask) 95mm (G St. L)	135/140 mmCW (Alaska)

Table 1 cont.

Scientific name	*Chionoecetes tanneri*	*Chionoecetes opilio*	*Chionoecetes bairdi*
Age of recruitment	9-10 yr	7-8yr (Sainte-Marie et al 1995)	5-6 yrs (Donaldson et al 1981)
Min size for Breeding	2 distinct breeding sizes for prim./multip (Somerton 82)	Male 40.4 fem 39.6 (Sainte-Marie 92) male 52 or >90 for multiparous(Conan& Comeau 86) Fem 40.3 (Jewit 81)	120mm (Donaldson 80) 65-100, primiparous 110mm for multiparous (Paul et al 83)
Size at 50% Morphometric Maturity	110-115 mm CW 50-70mm(Donaldson 92) Males 119, Fem. 79 (Pengilly 96) Alaska	80mm (Elner 82)	90-140mm (Brown 72) 108.9 w/117e Berring Sea (Somerton 81)
Egg extrusion	March - June(B.C.)	Feb-Mar primiparous Apr.-May multiparous (Elner 83) Atlantic	Jan-April (Paul 95) Alaska
Breeding	spring	Feb - May	late spring
Reproductive cycle	1 year ?	1 year	1year to 18 months
Fecundity	86,500 (Somerton and Donaldson 1996)	1200-12800 eggs (Elner 83)	50.000-500,000 (Somerton and Meyers 1983)
Larvae	planktonic (assumed)	planktonic	planktonic

Table 1 cont.

Scientific name	*Chionoecetes tanneri*	*Chionoecetes opilio*	*Chionoecetes bairdi*
Larval period	2 -3 months(Peryra 68) Jan-Jun off Oreg.	3-5mo. (Atlantic)	2-3mo(Lough74)
Spawning migration	males move to deep water (Peryra 68) Females move shallower (Jamieson 1990) No movement (Somerton and Donaldson, 1995)	Females move shallow for mating (Lovrich 93)	mating agregations observed (Stevens and Haaga, 1993)
Juvenile depth	640-1500m (Pereyra 68)	Shallow 50-80m (Lovrich et al 1995)	Shallow (<100m)
Habitat	deep water, fine sand green mud, rock	adults - fine sediments juv. coarse, cobble	adults - fine sediment juv. coarse; cobble

FISHERY PERFORMANCE

HISTORY OF FISHERY PERFORMANCE EAST COAST

In Atlantic Canada, Snow crabs (*Chionoecetes opilio*) have been managed by harvesting only males with carapace widths greater than 95 mm. The prohibition of harvesting females and males less than 95 mm carapace width was made with the intention of protecting the stocks from recruitment overfishing, as the females were not harvested, and the males were thought to mature and mate successfully before attaining the minimum legal carapace width. However, Conan et al. (1988) observed males over the minimum legal size that were not morphometrically mature, and some mature males that were below the minimum legal size, in a terminal molt, meaning that they may never reach harvestable size, but they can reproduce. Also, it was thought that morphometrically mature males under 95 mm carapace width were unable to mate with the multiparous females, the most important contributors to stock reproduction, and those morphometrically mature males over 95 mm carapace width were immediately caught in the fishery, perhaps before mating with multiparous females. (Hare and Dunn 1993) The Canadian Atlantic Fisheries advisory Committee (CAFSAC) expressed concern that the minimum legal size may not entirely protect the reproductive capacity of the stocks (CAFSAC 1989). By this time (mid- to late 1980's), most of the Snow crab stocks were fully exploited, and dependent on new recruitment each year. However, because growth and molting were not well understood, recruitment could not be forecast, and catches and stock sizes could not be accurately predicted.

Prior to 1988, annual quotas for southwestern Gulf Snow crab were set using Leslie Analysis. However, there were major deficiencies with this method, as a major assumption was violated (Hare and Dunn 1993). In the late 1980's this was refined by using a series of Leslie Analyses for separate components of the total fishing area. Also, post-fishery bottom trawl surveys were developed in 1988 to estimate the annual stock biomass and recruitment in the mid-Gulf and PEI. These surveys were expanded to the entire southern Gulf fishing areas in 1990 (AFSSR 96/1).

In the southern Gulf of St. Lawrence, landings gradually increased from the beginning of the in-shore fishery in the 1960's to 15,700 t in 1979. This fishery peaked at 30,500 t in 1982, and remained over 25,000 t until 1986. In 1987, landings declined to under 12,000 t and further declined to 7,000 t in 1990. In 1991 and 1992, landings increased to 12,695 t and 15,030 t respectively. (Hare and Dunn 1993). By 1994 and 1995, landings in the southern Gulf of St. Lawrence stabilized at the annual quota of 20,000 t. The most recent post-fishery trawl surveys indicate the end of a recruitment wave in the southern Gulf of St. Lawrence (AFSSR 96/1).

In the northwest Gulf of St. Lawrence, and St. Lawrence River estuary, Snow crab stocks show abundance fluctuations on an approximate 8 year cycle (AFSSR 96/6). These cycles consist of three consecutive years with decreasingly smaller numbers, referred to as a recruitment troughs, followed by five (at most) consecutive years with moderate to high numbers, referred to as recruitment waves. Research is continuing on the causes of these abundance cycles, and it appears that fishing is not the primary factor. Explanations offered include: a periodic change in the survival rate in one year-class, because of strong competition for space and food in the limited habitat of very young Snow crab; or a periodic variation in larval production.

The Snow crab fishery in this area began in the 1960's. Landings increased dramatically from 1979 to 1985, when effort and geographic extent substantially increased. From 1987 to 1989, landings declined from 5,255 t to 2,622 t, with declining CPUE and increased proportion of soft-shelled crab. This was the result of the recruitment trough of the 1977-79 year classes. In 1990-91, the proportion of soft-shelled crab decreased, CPUE increased, and landings increased, to a record peak of 7,245 t in 1995. This is the result of the 1980-84 recruitment wave. It is expected that the recruitment trough seen in the 1985-87 year classes would lead to a decline in CPUE and size of males in the catch, as well as general aging of the population in the 1995-97 fishery. Fishery data and research surveys confirm the expected declining trends (AFSSR 96/6).

On the east coast of Newfoundland, there was a collapse of the Snow crab fishery in the mid-1980's, near the Avalon Peninsula (Taylor et al 1994). This fishery began in 1979 in a shallow water area (< 200 m). Exploitation rates remained within the recommended levels of 50-60% of annual production between 1979 and 1981. Landings peaked in 1981 at 8,609 metric t and collapsed to 74 t in 1985. This collapse in landings off the Avalon Peninsula was accompanied by substantial declines in effort (480,000 trap hauls in 1981 to 17,000 trap hauls in 1985), CPUE (23.2 kg/trap haul in 1980 to 3.7 kg/ trap haul in 1985), and proportion of new-shelled (recently molted) crab (>80% in 1981 to < 20% in 1983-84). Water temperatures in this area ranged from -0.3 °C to -0.8 °C from 1978 to 1982. In the last half of 1982, bottom temperatures plummeted to a low of -1.6 °C, and rarely reached above -1.0 °C between mid-1982 and 1986, with the exception of two weak warming periods in 1983 and 1984. During the same time in Bonavista Bay, northwest of the Avalon Peninsula, in an area that has been consistently overexploited (Taylor and O'Keefe 1987), CPUE declined from a peak of 11.6 kg/trap haul in 1981, but stabilized at 4.1 to 8.2 kg/trap haul between 1982 and 1985, despite a doubling in effort during this period. Landings ranged from 1805 t in 1981, to a low of 905 t in 1986. Bonavista Bay is much deeper (220-486 m) on the commercial crab grounds than the crab grounds off the Avalon Peninsula (174-200 m), and Taylor et al (1994) suggests that the greater depth may have reduced the cooling effects of the Labrador Current. Taylor et al (1994) also suggests that in order to prevent future declines of the magnitudes seen off Newfoundland in the 1980's, it is advisable to monitor temperatures, catch rates, and crab shell conditions more closely on a seasonal basis. They also state that regardless of exploitation levels, temperature shifts likely affect molting and recruitment to such an extent that assumptions regarding long-term sustainability of annual landings are not justified.

Since the early 1990's, landings have increased dramatically in all areas of the Newfoundland Snow crab fishery, along with an increase or stabilization of the commercial catch rate (with the exception of Labrador and NE Newfoundland (AFSSR 96/15). However, there has been a notable increase in the proportion of old-shell crab in several areas, as well as a decrease in the catch of small-clawed crab, indicating declining recruitment and low exploitation rates on an aging standing stock. It is expected that a general decline in commercial catch rates will be evident in the next few years.

As in Newfoundland, there was an apparent collapse in the Eastern Nova Scotia Snow crab fishery off Cape Breton Island in the mid-1980's. Landings peaked in 1979 at 1,634 metric t, and plummeted to 89 t by 1985 (Tremblay et al 1994). This was accompanied by declining CPUE (28.7 kg/trap haul in 1979 to 8.6 kg/trap haul in 1984) and total effort (56,900 trap hauls in 1979 to 10,200 trap hauls in 1985). Between 1987 and 1993, landings increased (361 t in 1987 to 2,016 t in 1993), CPUE increased (12.6 kg/trap haul in 1987 to 32.5 kg/trap haul in 1992) and total effort increased (28,700 hauls in 1987 to 71,700 hauls in 1993). In 1994 and 1995, landings decreased to 1,574 t and 1554 t respectively. The large increases from 1987 to 1993 are attributed (Tremblay et al 1994) to three factors: (i) real increase in biomass: (ii) expanded fishing grounds; and (iii) increase in total effort. The explanation for changes in abundance of Snow crab advocated by Tremblay et al (1994) involves a fishing-induced shift in age structure. Initially there was a large biomass of older, slower-growing crab, likely in terminal molt. The high initial biomass resulted in initial high catch rates, which were sustained for about three years. Removal of the large old initial biomass resulted in a large reduction in landings and catch rates. However, removal of the older crabs increased survivorship of younger rapidly growing crabs, which entered the fishery between 1986 and 1990. Management of these fisheries from 1982 to 1993 was based strictly on effort controls, due to the difficulty in setting quotas where recruitment was unpredictable. These controls included seasonal openings (late summer to early fall), limited entry and the restriction of 30 traps/licence. In 1995, managers introduced individual boat quotas (IBQs) for regular licences in all areas .

HISTORY OF FISHERY DEVELOPMENT IN ALASKA

The Alaska Tanner crab fishery began in 1961, and grew into a major commercial fishery. Two of the four species tanner crab occurring in the North Pacific and Bering Sea *Chionoecetes bairdi* (tanner crab) and *Chionoecetes opilio* (Snow crab) form the bulk of the commercial fishery. There were record harvest levels of *C. bairdi* in 1978 of 123 million pounds, and 332 million pounds for *C. opilio* in 1991 (ADFG 1995).

In the Bering Sea, the commercial harvest of *C. bairdi* has had large fluctuations, with over 70 million pounds in 1969, declining to about 23 million pounds in 1973, increasing to 78 million pounds in 1977, collapsing to 5 million pounds by 1983, and no harvest in 1986 and 1987. The fishery recovered to almost 52 million pounds in 1991, and again collapsed to 1.8 million pounds by 1996 (Fig 4). The results of NMFS bottom trawl

surveys are used to set the pre-season guideline harvest level of *C. bairdi* in the Bering Sea. The abundance estimates from the NMFS bottom trawls, along with the recommended guideline harvest levels and annual catches are shown in Table 2. (Witherall 1996).

The record harvest in the Western Aleutians was 2.5 million pounds in 1977, followed by a decreasing trend, with minor peaks of 0.7 million pounds in 1982 and 0.3 million pounds in 1989. The 1991 harvest was merely 50,000 lb. in the Eastern Aleutians, and 8,000 lb. in the Western Aleutians (Fig 5) There was no harvest in either area in 1995 (Witherall 1996).

The Bering Sea *Chionoecetes opilio* fishery was first reported in 1970, at 2.1 million pounds, increasing to 7.3 million pounds in 1973, and collapsing to 0.5 million pounds in 1974. The fishery increased substantially in the late 1970's and stabilized until the mid-1980's, followed by huge increases exceeding 100 million pounds in the late 1980's. In 1991, the record harvest was 328 million pounds in 1991, followed by steady decreases to 65.7 million pounds in 1996. (Fig 6) From 1965 to 1980, the Bering Sea tanner crab fishery (*C. bairdi* and *C. opilio*) included the foreign harvest. (ADFG 1995) By the early 1970's allocations for the foreign fleet were sharply curtailed, and in 1976, legislation limited foreign fishing in U.S. waters. The results of NMFS bottom trawl surveys are used to set the pre-season guideline harvest level of *C. opilio* in the Bering Sea. The abundance estimates from the NMFS bottom trawls, along with the recommended guideline harvest levels and annual catches are shown in Table 3 (Witherall 1996).

Chionoecetes tanneri (grooved Tanner crab) and *Chionoecetes angulatus* (triangle Tanner crab), both deep water (> 400 fathoms) species have been commercially harvested only in the past few years.

The State of Alaska has established five Tanner crab registration areas: A - Southeastern Alaska Area; D - Yakutat Area; E - Prince William Sound Area; H - Cook Inlet Area; J - Westward Area. Each registration area may be designated as superexclusive or nonexclusive. Areas A, E and H are designated superexclusive, and Areas D and J are nonexclusive. However, there is the Norton Sound Superexclusive Area within Area J, which is presently closed to the tanner crab fishery. A vessel registered for a superexclusive area is limited to only that area for the year, and vessels registered for a nonexclusive area is excluded from the superexclusive areas, but a vessel may register for more than one nonexclusive area. (Alaska Administrative Code, Title 5, Ch. 35, Art. 01).

Legal catch is restricted to males with a minimum 140 mm carapace width for *C. bairdi* (Alaska Administrative Code, Title 5, Ch. 35, Art. 02), with the exception of Prince William Sound, where the minimum carapace width (CW) is 135 mm (Alaska Administrative Code, Title 5, Ch. 35, Art. 07), 127 mm minimum CW for *C. tanneri* , and 78 mm minimum CW for *C. opilio*. *C. bairdi, C. tanneri* and *C. angulatus* are managed as separate stocks in each of the registration areas. Management measures, such as

legal gear, effort, target species, harvest levels, and season openings, vary by registration area and are listed in Table 4.

The maximum harvest levels are set differently in each area, as noted in Table 4. In Area A, a Total Allowable Catch (TAC) is set at 2 million lb, in Areas D and E, the TAC is set at 1 million lb. However, In Areas H and J, and pre-season Guideline Harvest Level (GHL) is set based on an exploitation rate of the legal sized male abundance estimates from NMFS bottom trawl surveys. In Area J, this is based on a 40% mature male harvest rate for *C. bairdi* and, 58% mature male harvest rate for *C. opilio*. (Witherall 1996).

The Bering Sea Tanner crab stocks are managed by the State of Alaska through a federal Bering Sea/Aleutian Islands King and Tanner crab fishery management plan (Witherall 1996). There are three categories of management measures: Category 1 - Measures fixed in the fisheries management plan; Category 2 - Measures frameworked in the fisheries management plan so the state may change criteria outlined in the fisheries management plan; and Category 3 - Measures at the discretion of the state. These categories are outlined in Table 5. The guideline harvest levels in Category 2 are set by the State of Alaska. The 'Other" management measures in Category 3, includes state requirements for vessel permits and licences, and registration for each fishery and each area.

C. bairdi and *C. tanneri* are managed as 6 separate stocks in the Westward Area (Area J): eastern Bering Sea; eastern Aleutian Islands; and western Aleutian Islands; south peninsula; Chignik and Kodiak. The Snow crab (*C. opilio*) is managed as one stock throughout the Bering Sea/Aleutian Islands. The Bering Sea *C. bairdi* stock is currently at a very low abundance. Since 1991, when the total catch was 158% of the guideline harvest level, the total catch plummeted from 51.8 million lb. to 1.8 million lb. in 1996 (Table 2). The 1996 catch was only 29 % of the guideline harvest level. The 1995 NMFS bottom trawl survey showed very low levels of juveniles, pre-recruits, females and large males, with little chance on improvement in coming years (Witherall 1996).

In the Aleutians, there was a very limited *C. bairdi* fishery due to declining stocks. Alaska Department of Fish and Game trawl surveys showed a dramatic decline from 1991 to 1994. The fishery has been closed in the Kodiak District since 1994 and in the Chignic and South penninsula Districts since 1990. No landings were made in 1995 in either the Eastern or Western Aleutians. In 1996, no landings were made in the eastern Aleutians, and very limited landings were made in the Western Aleutians.

The Bering Sea *C. opilio* stocks appear to be recovering as abundance estimates of large males from NMFS trawl surveys increased dramatically in 1996. In addition, the 1995 NMFS bottom trawl surveys indicated an 88% increase in the number of pre-recruits and a 44% increase in the number of females. The 1997 guideline harvest level for Bering Sea *C. opilio* stocks is set at 117.0 million pounds.

There is a developing fishery for *C. tanneri* in Area J (Westward Area), with a proposed 1997 harvest limits of 200,000 lb. in the Bering Sea, 200,000 lb. in the Eastern Aleutians, 200,000 lb. in the South Peninsula, 100,000 lb. in the Western Aleutians, and 100,000 lb. in the Kodiak district. (ADFG 1997). This is based largely on the historic harvest levels and trends in CPUE. In other areas, the 1997 guideline harvest level is set at 100,000 lb. to accommodate exploratory fisheries. There are gear modifications specified to address concerns on the viability of deepwater crabs discarded at sea because of size and sex restrictions. Also, there is no restriction on vessels registered in superexcluded areas from participating in this fishery, as noted in Table 4.

Table 2: Abundance estimates (millions of large males (.135 mm CW), recommended preseason guidline harvest levels (million lb), and total catches (millions lb.) of Bering Sea C. bairdi, 1980-1996 (from Witherall 1996)

Year	Abundance of males (>135 mm CW) (millions)	Guideline Harvest Level (million pounds)	Total Catch (million pounds)
1980	31.0	28 - 36	23.8
1981	14.0	28 - 36	29.6
1982	10.1	12 - 16	11.0
1983	6.7	5.6	5.3
1984	5.8	7.1	1.2
1985	4.4	3.0	3.1
1986	3.1	0	0
1987	8.3	0	0
1988	17.4	5.6	2.2
1989	42.3	13.5	7.0
1990	53.7	72.3	45.9
1991	45.5	32.8	51.8
1992	52.8	39.2	35.1
1993	27.2	19.8	16.9
1994	20.0	7.5	7.8
1995	13.3	5.5	4.2
1996	12.5	6.2	1.8

Table 3: Abundance estimates (millions of large males (> 102 mm CW), recommended pre-season guidline harvest levels (millions of lb.), and total catches (million lb.) of Bering Sea C. Opilio, 1980-1996 (from Witherall 1996).

Year	Abundance of males (>102 mm CW) (millions)	Guideline Harvest Level (million pounds)	Total Catch (million pounds)
1980	na	na	39.6
1981	na	39.5 - 91.0	52.8
1982	na	16.0 - 22.0	29.4
1983	na	15.8	26.1
1984	226.9	49.0	26.8
1985	115.7	98.0	66.0
1986	128.9	57.0	98.0
1987	221.0	56.4	101.9
1988	261.1	110.7	134.0
1989	268.2	132.0	149.5
1990	608.7	139.8	161.8
1991	807.0	315.0	328.6
1992	420.8	333.0	315.3
1993	212.9	207.2	230.8
1994	111.9	105.8	149.8
1995	99.9	73.6	75.3
1996	236.5	50.7	

Table 4: Management measures by Registration Area for Alaska Tanner crab (C.bairdi)

Registration Area	Pot Restrictions	Maximum Harvest Level	Season	*C. tanneri* & *C. angulatus* Restrictions
A - Southeast Alaska (Superexclusive)	Separate pot & ring net reg'n: no less than 96% from pots	2 million lbs	Feb 15 - May 1	> 200 fathoms; pot only
D - Yakutat (Nonexclusive)	Not more than 100 pots & ring nets combined	1 million lbs	Jan 15 - May 1	>200 fathoms; pot only Varied season. Participants in superexclusive fisheries are not excluded from this fishery
E - Prince William Sound (Superexclusive)	Not more than 75 pots ; ring nets permitted	1 million lbs	Jan 15 - Mar 31	
H - Cook Inlet (Superexclusive)	Not more than 75 pots ; ring nets permitted	Guideline Harvest Range to be determined	Jan 15 - Mar 31	
J - Westward (Nonexclusive - single district restriction)	Pot only	Guideline Harvest Range to be determined		
Kodiak	75 pots		Jan 15 - Mar 31	75 lg. pots or 150 sm. pots
Chignik	75 pots		Jan 15 - Mar 31	150 lg. pots or 300 sm. pots
S. Peninsula	75 pots		Jan 15 - Mar 31	150 lg. pots or 300 sm. pots
Bering Sea	250 pots for vessel > 125 ft 200 pots for vessel < 125 ft		E. Aleutians: Jan 15 - Mar 31 W. Aleutians: Nov 1 - Mar 31 W. Bering Sea: Jan 15 - Mar 31 E. Bering Sea: Nov 1 - Mar 31 *C. opilio*: Jan 15 - Closure order	> 200 fathoms, pot only Varied season. Participants in superexclusive fisheries are not excluded from this fishery

Table 5: Management measures implemented for the Bering Sea/Aleutian Islands King and Tanner crab fisheries, as defined in the federal crab fisheries management plan, by category

Category 1: Fixed in FMP	Category 2: Frameworked in FMP	Category 3: Discretion of the state
Legal Gear	Minimum size limits	Reporting requirements
Permit Requirements	Guideline harvest levels	Gear placement and removal
Federal observer requirements	Inseason adjustments	Gear storage
Limited access	Districts, subdistricts and sections	Gear modifications
Norton Sound superexclusive registration area	Fishing seasons	Vessel tank inspections
	Sex restrictions	State observer requirements
	Closed waters	Bycatch limits
	Pot limits	Other
	Registration areas	

Figure 4: Commercial Harvest - Bering Sea Tanner Crab (C.bairdi)

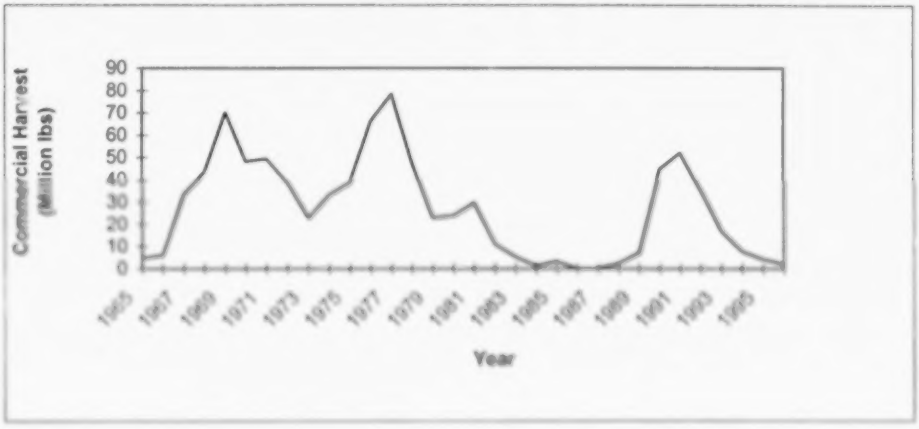


Figure 5: Commercial Harvest - Aleutian Islands Tanner Crab (C.bairdi)

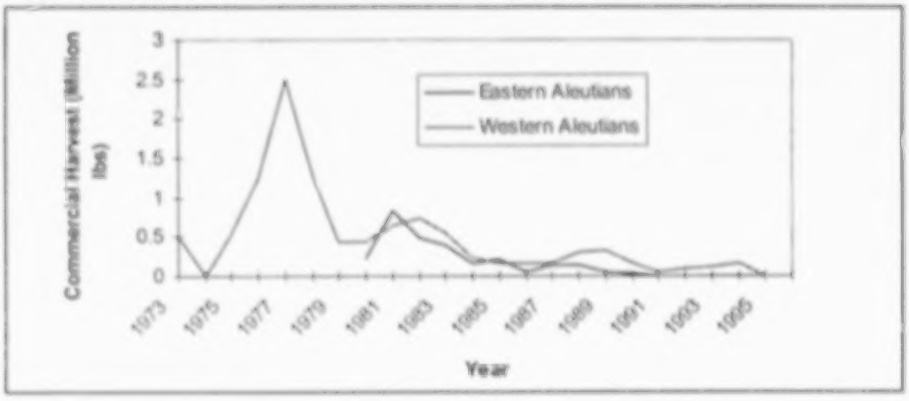
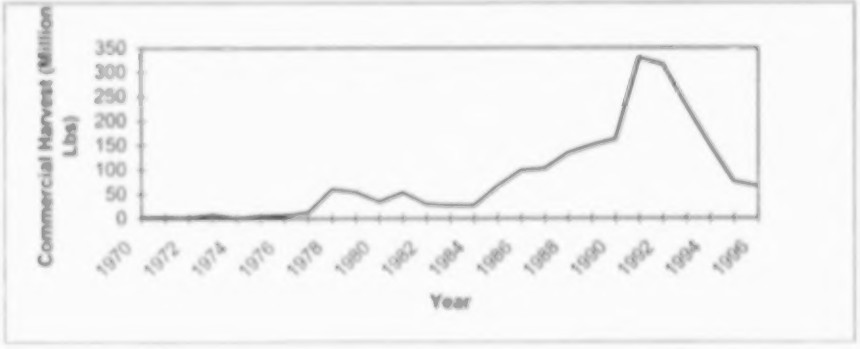


Figure 6: Commercial Harvest - Bering Sea Snow Crab (C.opilio)



PRECAUTIONARY DEVELOPMENT

BIOLOGICAL CONSIDERATIONS

Kruse (1993) observes that life history traits are often related (Adams, 1980; Hoenig, 1983) and characterizes three different fisheries in Alaska based on biological traits of the individual species. Dungeness crab (Cancer magister), tanner crab (*Chionoecetes bairdi*) and red king crab (*Paralithodes camtschaticus*) are classified as *R* or *K* selected species according to MacArthur and Wilson's (1967) criteria where *R*-selected species tend to have low age at maturity, small maximum size , high M, low maximum age and perhaps higher fecundity, and *K*-selected species exhibit opposite traits. By these criteria, Dungeness crabs appear the most R-selected, while red Kings appear most K-selected with tanner crabs falling in between. It should be emphasized that these traits are relative and not entirely consistent within the species considered. For instance, Dungeness crabs have high growth and mortality rates (R-traits) but exhibit relatively large size and are reproductively complex; king crabs are the longest lived, slowest growing with the lowest M of the three crabs but exhibit relatively high fecundity and are not as K-selected as ocean perch, (*Sebastes aleutus*) (Leaman, 1991). Some specific traits are notable as they may apply to *Chinoecetes tanneri*. In particular, large size at maturity, slow growth, relatively long lifespan and sophisticated reproductive strategies (Adams, 1980) are K-selected traits. Generally speaking, populations of K-selected species tend to be more stable, produce higher yields at later recruit ages and lower fishing mortalities, have lower standing stocks and are more susceptible to overfishing and stock depletion (Kruse 1993; Perry 1997 submitted). These considerations should be a part of any management plan developed for *C. tanneri*.

Fishing may also have negative and destabilizing effects on normal biological compensatory mechanisms. For instance, shifts in the character of the reproductive population by removal of large male crabs may have a negative effect on reproductive potential (Paul, 1984; Bailey and Elner, 1992; Kruse, 1993). This may occur because older, multiparous females unable to be bred by small male crabs continue to prevent recruitment of primiparous females to the breeding population. The result is a senescent population with low reproductive potential. Kruse (1993) recommends reconsidering the merits of male only fisheries. Murphy (1968) suggests that iteroparity (the ability to spawn repeatedly) is an evolutionary response to environmentally induced variation. Multiple spawning times and strategies exhibited by *Chionoecetes* is a form of iteroparity. The response of heavily exploited stocks (Murphy, 1968) is often a trend towards uniparity, a condition which makes the stocks highly vulnerable to unfavorable environmental influence. Sainte-Marie et al (1995) cautions that careful interpretation should precede any statements about efficacy of regulations.

MANAGEMENT STRATEGIES

Target Reference Management

Hilborn and Sibert (1988) identify a "prescription for disaster" for a developing fishery where fisheries management is based on the assumption that catch will continue to increase with increasing effort reaching a maximum yield, which can then be sustained. Under this paradigm, they describe the nearly inevitable development path of excess effort leading to declining catch rates and finally economic collapse of the fishery. The main problems appear to be recognizing when maximum harvest has been achieved, and responding in time to reverse the trend. Catch rates are inevitably higher during development, so that a fishery which appears profitable at the outset may not be economically feasible once sustainable levels are reached. Compounding the problem are naturally occurring variations in the level of abundance of the target species. Caddy and Gulland (1983) list four basic types of variation; steady state, cyclical, irregular or spasmodic. Attempting to manage a fishery without reference to patterns of fluctuation will be futile. Hilborn and Sibert (1988) refer to this paradigm shift as "tracking the moving mountaintop" rather than continuing up a gradual slope to rest on the summit . They point out that the summit is only recognized once it has been exceeded and you are on the way down. The mountaintop may not only be moving, but changing its height and slope as well. Risk averse management would estimate when the mountaintop is being approached by measuring diminishing returns to scale and stopping development on the basis of that diminishment (Walters, 1996).

Management on the basis of MSY (maximum sustainable yield) or TRP's (target reference points) depends upon ability to accurately assess the stock. Given the low precision of assessment methodologies (McDaniels 1996; Kruse, 1995), the use of TRP's often leads to excessive and often hard to reverse overshoots in levels of exploitation (Caddy and McGarvey, 1996). Management by some biological threshold reference (Quinn et al, 1990: Zheng et al. 1993; Caddy and McGarvey, 1996) independent of stock size is preferable. In this approach, fishery performance and response of the fished population is monitored and specific management actions are taken once threshold levels are reached (Perry et al, 1997).

Other strategies

In Alaskan fisheries, the trend in recent years has been away from 2-S and 3-S (Size, Sex, and Season) management towards preseason guideline harvest levels based on preseason stock assessment surveys, or historical performance, or in-season fishery

performance. (Pengilly, pers.com., Kruse, 1993) King and tanner stocks managed by 2-S and 3-S in many cases no longer support fisheries (Kruse, 1993). Of particular note, are the varied responses of crab stocks to similar management regimes (Kruse, 1993; Elner and Robichaud, 1986) which have raised doubts about management strategies. Massive collapses of congeneric stocks in Alaska (Colgate, 1982) have sensitized managers to the instability of single sex fisheries for *Chionoecetes* (Conan et al. 1990). Conan et al. (1990) state that "it is important to stress that fisheries management cannot be efficiently achieved on the basis of simplified or erroneous biological information" and that "modeling cannot supplement the lack of information or inaccurate information." It has become apparent that a clear understanding of growth, maturation and reproductive processes is essential to the proper management of *Chionoecetes* stocks (Elner and Robichaud, 1986; Comeau et al, 1991).

The importance of acquiring this type of information early in the developmental stage of the fishery cannot be overemphasized. Most of our assessment methods are estimates of depletion (Walters, 1996) depending on contrasts between data collected over time. Failure to provide population estimates at the outset of a fishery will forego a crucial benchmark for gauging depletion. Once a fishery has been established, it is generally impossible to go back and obtain that information.

CPUE

Changes in CPUE, especially in trap fisheries, are generally poor estimators of abundance due to the influences of different gear performance, changes in fishing patterns and efficiency (often undocumented), and changes in the behavior of the target species. CPUE data is usually not transferable between areas or over time and is therefore unlikely to provide a precise measure of stock abundance. Nevertheless, CPUE is the only type of information likely to be generated by a trap fishery, and every effort should have to be made to standardize gear and to index catches to population.

Monitoring fishing activity alone does not solve the indexing of abundance problem (Walters, 1996). Fisheries independent information is required, especially during early development that will provide a clear indication of the dimensions of the stock, the spatial variability and ranges in abundance. Otherwise, serial depletion of the resource may occur where concentrations are targeted and depleted, yielding no information about unfished areas or about the extent of depletion. An example is the sea cucumber fishery in B.C. prior to 1996 (Boutillier and Campbell, 1996). Catch records showed little sign of decrease in CPUE because of the cucumbers' tendency to form dense aggregations and the fishers tendency to move once CPUE declined (i.e. the patch was harvested). The concept of "exploratory fishing" implies just this type of fishing activity and should not be used in the context of risk averse fishery development.

Precautionary Approach to Management

The FAO document, a Precautionary Approach to Fishery Development, "recognizes that fisheries systems are slowly reversible, poorly controllable, not well understood and subject to changing human values". It is also noted that "most problems affecting fisheries result from insufficiency of precaution in management regimes when faced with high levels of uncertainty encountered in fisheries". Hilborn (1987) refers to uncertainties encountered in new fisheries as "surprises" and management responses should include reference areas and broad monitoring programs. In developing a management plan, (FAO 1996) it is stated that " to be precautionary, decision rules are required for responding to unexpected or unpredictable events with minimum delay." One of the major problems facing managers is the time lag between recognizing the need to reduce effort, and the time required for fishers to admit a problem exists. This problem is exacerbated by a tendency for governments to subsidize fisheries perceived to be under economic decline (Caddy and Gulland, 1983). Effort, established during a time of high fishery abundance, can then, through subsidy, survive a period of low returns. If and when catches return to normal, increased effort is applied without a diminishing of the initial fleet. The result is a ratchet effect which allows increasing effort but not the reverse. An adaptive management strategy takes these tendencies into account. It is composed of two elements (Hilborn and Sibert, 1988), a monitoring system to measure effort and to estimate stock size (stock assessment) and a response system that allows effective control of effort as biological and environmental variables change. Management should be able to adapt rapidly to what the stocks are doing given that predictive capabilities in a developing fishery will initially be low (Miller and Elner, 1993).

WHAT CAN BE EXPECTED OF A FISHERY FOR C. TANNERI

Little is known of the commercial distribution or seasonal availability for this species. A learning phase is anticipated as fishers come up to speed during which time wild fluctuations in CPUE will occur (R. Elner, pers. com.) which may not reflect relative abundance accurately. After this phase CPUE values will likely become more comparable and catches are expected to vary as the stock(s) are mapped. The developmental (phase 2) may be marked by downward trends in CPUE, size/age composition or both (Jamieson, pers. com.) depending on the harvest strategy developed. Fluctuations in abundance and age composition over time as a natural occurrence are to be expected. Catch rates during a sustainable fishery will likely be lower than during initial development.

The ecosystem of which *Chionoecetes tanneri* is a dominant member, is dependent on a transfer of energy generated locally by near-surface primary production over the continental shelf. Population dynamics are ultimately regulated by this energy flow and overall fishery production will likely be lower than that of a comparable shallow water ecosystem sustained directly by primary production. *C. tanneri* is relatively longer lived and probably has a lower natural mortality rate than a shallow water species such as Dungeness crab, therefore, sustainable fishery potential may not be large. Based on a wealth of examples from other similar fisheries, failure to carefully control effort could result in collapse of this fishery.

CONCLUSIONS

GENERAL CONCLUSIONS

As biologists, we are in the enviable position of beginning a fishery while the stock is at or very near MB_0 (natural mortality rate at a virgin biomass state). That assumes mortality from other fisheries or other anthropogenic causes is negligible, which appears to presently be the case off British Columbia. No other fisheries have impacted the lower slope region to date in which bycatch mortality is a factor. The same cannot be said for the fishery off Oregon where it is estimated that annual allowable harvest may already be achieved by the slope bottom trawl fishery (Oregon Dept. of Fish and Wildlife staff report 1994). Similarly, the State of Alaska has only limited data from one pre-fishery trawl survey (Somerton and Donaldson, 1996). This being the case, we cannot afford to forego collection of vital information at the outset of the fishery that will be forever lost once a fishery is established (Caddy and Gulland, 1983). Throughout the development of a new fishery for *C. tanneri*, there needs to be strong interaction among science, management, and stakeholders in order to provide scientific advise for precautionary management (Perry et al, 1997 in preparation).

From what we know of present fisheries for *C. tanneri*, and what can be surmised from the literature and histories of fisheries on King and Tanner crabs, it is clear that management by size and sex alone is insufficient to ensure a sustainable fishery. The theory that removal of only those crabs that have been allowed to breed may be sound, but selection by carapace width alone does not ensure that this occurs. Other aspects of the reproductive biology and stock dynamics of this species must be taken into account in managing this fishery.

Male requirements for breeding, aside from sexual maturity include, sufficient shell hardness, sufficient size and sufficient claw development to effectively compete for and breed female crabs. Because markets generally favor large crabs, and because of marked sexual dimorphism, the fishery for *C. tanneri* will undoubtedly target large male crabs. Several suggestions have been made that would better define the target, such as claw measurement to determine morphometric maturity (Safran et al, 1990), a ratio between carapace width and claw height (Conan and Comeau, 1986) that would be even more precise at determining morphometric maturity, and the use of a durometer (Safran et al, 1990; Hicks and Johnson, 1991) to ensure only hard shelled crabs are harvested. However, none of these measures have yet been proved practical in existing fisheries. Furthermore, the reproductive biology appears sufficiently complex that unless other factors are taken into account, such as the time interval between molting and breeding, (which may effectively be a year or more), size/maturity regulations may be defeated. Clearly, in addition to size regulation, some limit on effort will also be required to sustain a fishery for this species.

BASIC INFORMATION REQUIREMENTS

In order to effectively manage a developing fishery for Tanner crabs, there are certain basic parameters which must be known at the outset of the fishery or be acquired in the early stages of the fishery development. Obviously the more extensive our knowledge, the sounder the basis for management. However there are minimum information requirements which must be met before any effective long-term management strategy can be developed and before any fishery can proceed in a sustainable and risk averse manner. For guidance in this process, I rely heavily on recommendations presented by Perry, Walters and Boutillier in " A framework for providing scientific advise for the management of new invertebrate fisheries" (1999, in press). This framework explicitly endorses the precautionary approach to fisheries (Garcia, 1994; FAO, 1995) in which scientific advice provides the basis for setting initial, precautionary, management strategies. Feedback gained from scientific research during all phases of the fishery is used to tune management plans in order to decrease the risk to the resource through overexploitation while increasing potential benefits to stakeholders and the public (FAO,1995). Perry et al. (1999) list options for management strategies in which costs and risks are outlined, however the underlying basic data requirements for all the options are similar. These are outlined below.

Phase 1 Requirements

Phase 1 is the "Fishing for Information" stage during which the minimum knowledge needed to effectively manage a developing fishery is acquired. Information from this phase is used to develop management plans and to target fishing on areas that have the biological characteristics to sustain fishing (Perry et al. 1999, in press). Basic information required for *Chionoecetes tanneri* includes:

Resource Distribution

Intuitively, in order to set limits on fishing activity we must know or have a reasonable estimate of the resource distribution in both space and time. As simple as this initial concept may appear, it must be broken down into a series of new questions in order for the concept of population to have meaning. Only when the distribution(s) is known is it possible to obtain any estimate of biomass , or to apply any management strategies.

From the standpoint of stock management, it is necessary to answer the following;

1. Are we dealing with only one species? Fishers must be able to recognize species differences. *C. tanneri* and *C. angulatus* are sufficiently similar for confusion to occur.

2. Is the resource one continuous stock or numerous isolated populations in terms of recruitment, growth, reproduction and other biological parameters.

3. What is the geographical range of the population(s)?

4. What is the bathymetric range?

5. With reference to the above two questions, are there sexual and/or seasonal differences (i.e. is there migration)?

6. What is the distribution of juveniles?

7. What is the annual variability in these distributions?

Basic Biology and Life History

It is important to know basic life history, especially as it pertains to breeding times, molt periods, and seasonal behavior. As mentioned above, it will be necessary to determine the distribution of juveniles and habitat of various life stages and the method of reproduction and recruitment of larvae. Equally important is knowledge of size at sexual maturity and morphometric maturity for both males and females, the size range over which functionally reproductive adults occur and the period of the reproductive cycle.

Population size/ Age structure

From the size/age structure of the crab population it is possible to infer lifespan, growth and mortality rates. The structure of the population prior to fishing can be used as a benchmark in estimating fishing effects and may also indicate potential biomass available for harvest during initial stages of the fishery. Initial high yields in the fishery may be the result of mining an accumulation of large, slow growing individuals. In particular, it is necessary to determine whether *C. tanneri* has a terminal molt, as this will have different implications to harvesting than if they are able to continue growth past morphometric maturity. A terminal molt means the population of reproductively mature crabs will continue to age but not to grow. The spatial structure of the population components is also important if the fishery is to target mature crabs that have had the opportunity to breed. Reproductive behavior may also be affected by population structure in this species.

Estimation of Mortality Rates

An estimate of natural mortality is necessary for development of any management strategy based on either TAC or exploitation rate (Perry et al 1999, in press). This can be obtained from the empirical relationship between natural mortality and maximum age described by Hoenig (1993), from direct surveys where proportion at each age class are determined, from size frequency analysis, or through direct experimentation, and can be verified by long-term observation of the fishery. These estimates will in turn depend on

development of aging techniques involving tagging or other biological or elemental age estimators.

Recruitment Patterns

Knowledge of recruitment patterns, both temporally and spatially, annual reproductive success and natural fluctuations in recruitment over time is necessary. This information will be acquired as the fishery proceeds, but in order to forecast fluctuations in recruitment to the fishery, a knowledge of the population structure of immature crabs will be required. Data needs to be collected from the start of the fishery to be of value for long term management.

Knowledge of Fishing Effects

The impact of fishing activities on females and juveniles of the target species and of other species (bycatch) must be known. Important also is the fate of discards released at the surface. Displacement from original habitat and subsequent mortality due to handling, changes in pressure/temperature and predation may be substantial. An index of catchability with season will also be required if CPUE is to be considered as an indicator of relative abundance. It will also be necessary to ascertain the effect of fishing on crab population structure and dynamics, whether a density dependent relationship exists which could be altered if larger, older individuals are removed as will likely occur in a fishery for this species.

Phase 2 Requirements

Phase 2 is the fishing for commerce stage. During this time, information gathering initiated in the phase 1 stage will continue to be collected. This phase may also be used to test models or to initiate "experiments" from which to gauge stock response to different management strategies. Because there is little known about this species and its long-term response to fishing pressures, the establishment of "reference areas" (Perry et al. 1997) would provide both refuges from harvest, thereby limiting exploitation rate, and control areas against which to measure fishing impact. Reference areas would also provide biological information, such as mortality rates or natural population fluctuations which are independent of fisheries. Establishment of such areas will require biological knowledge from phase 1 fishing activities in order to be effective for the purposes intended and should include areas attractive to fishing. (Hilborn and Sibert 1988).

Modeling will assist management in developing fishing strategies. For review see Perry et al (1999, in press). Data from the fishery can then be used to test the model's predictions. Modeling will improve as more time series data are collected; detailed models developed from traditional fisheries may then be applied (Hillborn and Walters, 1992).

RECOMMENDATIONS

GENERAL BIOLOGICAL RECOMMEDATIONS

It is recommended that harvest criteria be developed with reference to reproductive biology. This may incorporate measurements of carapace width and claw height, intermolt state etc. to identify morphometrically mature crabs, but should reference other features such as size at functional maturity, frequency of molting, molt increments and female reproductive potential. Implications to the population dynamics of a male only fishery should also be considered.

A terminal molt should be assumed for both sexes until otherwise demonstrated.

Biologically sensitive periods, ie. spawning or softshell periods, should be identified and fishing prohibited during those periods.

Biologically sensitive areas, ie. areas critical to the survival of any life stage such as specific spawning or rearing habitats, should be identified and fishing activities in those areas either from a directed fishery for tanner crabs, or a fishery for another species, be prohibited or restricted.

Every effort should be made to minimize discard mortality from the outset.

Gear should be standardized from the outset.

PHASE 1 RECOMMENDATIONS

Information relevant to stock monitoring and management not obtainable from other sources must be collected during this initial "Fishing for Information" stage. This phase should be considered a fisheries independent assessment of crab stocks and may not be initially profitable. However, the long-term success or failure of this fishery may well be determined by the extent and quality of this initial data.

Resource Distribution

Delimiting the stock is of fundamental importance. Initial fishing efforts should focus on mapping distributions of all sectors of the population(s) of *C. tanneri*. This should be done in a methodical manner for the entire coast, identifying concentrations as well as areas of sparse abundance. Limited fishing on concentrations identified in this manner may be considered during this phase once distributions are defined. Fishing should be undertaken by some vessels throughout the year to identify seasonal shifts in populations and timing of biological events. Exploratory fishing only for profitable

concentrations of crabs should not be considered as an alternative to an extensive and scientifically appropriate population survey over the entire range of prospective habitat. Periodic re-evaluation of species distribution will be an ongoing commitment as the fishery develops.

Other Basic Information

All the other basic information will be generated to some extent during resource mapping. In order to obtain this information it will be necessary to sample extensively in all areas during all seasons both at sea and at point of landing. One hundred percent observer coverage of vessels engaged in mapping the resource should be considered since it is important to document in detail catch composition over the entire distribution. Small mesh traps designed to sample small crabs should be included as a part of all gear deployments over all areas to assist in this purpose. Further laboratory analysis of selected samples will be required and information relating shell condition to meat yields should be collected during shore based processing.

Collection of similar information on *C. angulatus*, *Lithodes couesii*, and *Lithodes aequispina* should also be undertaken at this stage, since future consideration of harvest for those species will require that information.

Specific Data Requirements

Vessel logbooks should be a mandatory requirement during all phases of the fishery. Logbooks should contain accurate georeferencing, depths of gear and information on gear types used, soak times, trap spacing and baits. A record of all traps pulled should include species composition of catch, number of discards by sex, number of crabs kept and total weight of landed crabs.

Data collected by onboard observers should include detailed catch information for all species caught. Specific information on Tanner crabs should include: shell width and claw height measurements (Fig. 7); identification of sex; reproductive condition; shell condition (age); injury evaluation; and incidence of disease or parasitism. Other information collected at sea may include: detailed morphometric measurement; weight measurement; evaluation of gonadal state; and intermolt state via mouthparts.

Laboratory analysis of samples may include morphometric measurement, microscopic evaluation of gonadal condition, estimation of fecundity, precise evaluation of intermolt state and shell age, incidence of disease and infection, and other physiological measurements.

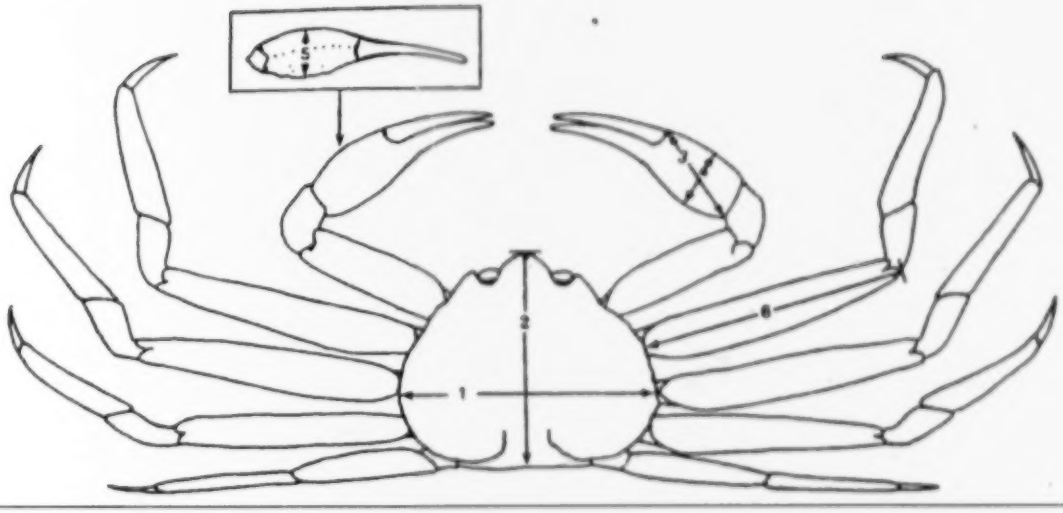


Figure 7: Standard measurements taken on male snow crab: 1. Cephalothorax length; 2. Cephalothorax width; 4. Chela height; 5. Chela width; 6. 2nd pereipod meropodite length. Dorsal view of chela is shown in rectangle

Other Requirements

It may be necessary to extensively sample some area of the crab distribution, or some life stage during some time period. For instance, in order to document benthic recruitment of juveniles, it may be necessary to fish beyond known depth distributions of adults. Tagging experiments should be considered during this phase to yield valuable information during subsequent development of the fishery as tags are returned during a time of increased fishing effort. The use of small meshed traps and other gear types (bottom trawls, plankton nets) should be considered to obtain additional information.

PHASE 2 RECOMMENDATIONS

Fishing abundance will be identified from phase 1 activities. It should then be possible to construct meaningful management areas to replace arbitrary ones selected during initial development. During phase 2, experiments should be undertaken to test models, to determine fishing effects and to develop references for stock estimation or other parameters. The fishery will target commercial concentrations, however there remains a commitment to continue population parameter evaluation outside those concentrations.

The establishment of closed reference areas is recommended. These should be appropriately sized and located (from phase 1) to act as functional population reserves. These should include areas attractive to fishing exploitation. Due to our uncertainty of the effects of fishing, these areas will serve not only to limit effort but to act as reference

points as the fishery develops while maintaining the potential for rebuilding stocks outside of these areas.

Adaptive management experiments should be initiated. It is recommended that some selected areas be fished at different exploitation rates to determine the response of the population and to test management strategies. This activity should occur as early in the fishery as possible in order to apply the knowledge gained to re-define management strategies.

During the "Fishing for Commerce" phase, collection of detailed catch, effort, depth and location information should continue. A high level of catch sampling should be maintained in order to supplement phase 1 information and to address specific requirements of management.

CONTROLLED FISHERY DEVELOPMENT

Fishery development should be undertaken jointly by all partners and will be overseen by a Federal/Provincial committee formed under the auspices of the MOU (which currently oversees the new Flying squid fishery) and which will ultimately determine the initial level of participation.

Market conditions will probably dictate a minimum Size and male Sex fishery with an added Seasonal or softshell restriction imposed by the Department based on biological findings from phase 1 and 2. Assuming that neither a reliable initial biomass estimate, nor a precise estimate of natural mortality will be available during initial stages of a commercial fishery, total effort should be restricted to a small number of vessels, and these in turn distributed between management areas. Allowable catch should be restricted to a conservative amount which would allow the participating vessels a marginal profit based on projected landed value of product and catch rates from previous fishing activities and from other Tanner fisheries. CPUE and population structure/composition in fished areas should then be closely monitored and a relative index of abundance developed to enable detection of change over the course of the initial fishery.

Based on the results of the first several years, effort/participation may be increased by stages allowing some return on investment for those involved in initial development phases. At the same time, certain management areas could be more heavily fished experimentally to determine at what level fishing effects can be detected and what form they take. Reserve areas should be resurveyed to detect natural fluctuations in population structure and provide contrast to biological parameters from fished areas. The effect of female removal should also be evaluated experimentally. It should be emphasized that this process will be iterative throughout development and subsequent management evolutionary based on the results of the fishery and biological findings.

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REFERENCES

REFERENCES CITED

Adams, A.E., 1982. The mating behaviour *of Chionoecetes bairdi.* In: Proc. Int. Symp. Genus *Chionoecetes*, pp 233-271. University of Alaska Seagrant Program, Fairbanks, Alaska.

Adams, A.E. and A.J. Paul, 1983. Male parent size, sperm storage and egg production in the crab *Chionoecetes bairdi* (Decapoda: Majidae). Int. J. Invert. Reprod. 6: 181-187.

Adams, A.E., 1980. The life history of the snow crab, *Chionoecetes opilio*: a literature review. Alaska Sea Grant Program, Sea Grant Report No.78:13. University of Fairbanks, Alaska.

Adams, A.E., 1985. Some aspects of reproductive biology of the crab *Chionoecetes bairdi:* Final project report. Alaska Sea Grant report 85-06, University of Fairbanks, Alaska.

ADFG. 1995. Annual Management Report for the Shellfish Fisheries of the Bering Sea/Aleutian Islands, Alaska Department of Fish and Game, Dutch Harbour office, June 1995.

ADFG. 1997. Proposed allowable harvest levels for the Westward Region *Chionoecetes tanneri* fisheries in 1997. Alaska Department of Fish and Game Memorandum 97-13. Feb 1997.

AFSSR 96/1. 1996. Stock Status Report on Southern Gulf Snow Crab. Department of Fisheries and Oceans Atlantic Fisheries Stock Status Report. Maritimes Region. 9p.

AFSSR 96/15. 1996. Stock Status Report on Newfoundland and Labrador Snow Crab. Department of Fisheries and Oceans Atlantic Fisheries Stock Status Report. Newfoundland Region. 5p.

AFSSR 96/6. 1996. Stock Status Report Snow Crab of the Estuary and Northern Gulf of St. Lawrence. Department of Fisheries and Oceans Atlantic Fisheries Stock Status Report. Laurentian Region. 13p.

Alaska Dept. of Fish and Game Summary of the 1994 mandatory shellfish observer program database. Regional information Rep. No. 4k95-32.

Alton, M. 1986. Fish and crab populations of the Gulf of Alaska seamounts. *In* R. H. Uchida, S. Hayes, and G.W. Boehlert (eds.) Environment and resources of Seamounts in the North Pacific, p. 45-51. U.S. Dep. Commerce., NOAA Tech. Rep. NMFS 43.

Armstrong, D.A., T.C. Wainwright, G.C. Jensen, P.A. Dinnel, and H.B. Andersen. 1993. Taking refuge from bycatch issues: red king crab (*Paratithodes camtschaticus*) and trawl fisheries in the eastern Bering Sea. Can. J. Fish. Aquat. Sci. 50: 1993-2000.

Bailey, R. and R.W. Elner, 1992. Northwest Atlantic snow crab fisheries: lessons in research and management. *In,* Marine invertebrate fisheries: their assessment

and management. J.F. Caddy ed. John Wiley and sons, Chidchester, England, pp. 261-280.

Barros, J.A., P.A. Tester, and R. Morita, 1978. Incidence, microscopy, and etiology of exoskeleton lesions in the tanner crab, *Chionoecetes tanneri*. Oregon Agricultural Experimental Stn. tech. paper no. 4847; 1141-1149.

Beninger, P.G., R.W. Elner, T.P. Foyle, and P.H. Odense, 1988. Functional anatomy of the male reproductive system and the female spermatatheca in the snow crab, *Chionoecetes opilio* O Fabricius (Decapoda: Majidae), and a hypothesis for fertilization. Journal of Crustacean Biology 8: 322-332.

Botsford, L.W., 1986. Population dynamics of the Dungeness crab (*Cancer magister*). Can. Spec. Publ. Fish. Aquat. Sci. 92: 140-153.

Boutillier, J.A., A. Campbell, R. Harbo, and S. Neifer, 1996. Scientific advice for the management of the sea cucumber (*Parastichopus californicus*) fishery in British Columbia. Pacific Stock Assessment Review Committee Paper 196-12. 28p.

Bower, S.M. and J.A. Boutillier, 1993. Diseases of spot prawns (*Pandalus platycerus*) caused by intracellular bacterium and a Hematodinium-like protozoa. J. Shellfish. Res. 12:135.

Boyle, L., L.C. Byrne, H. Moore and D.Pingelly, 1996. Alaska Department of Fish and Game Summary of th 1995 Mandatory Shellfish Observer Program Database. Regional Information Report No. 4K96-47

Brethes, J and F. Coulombe, 1989. Oriented movements of tagged male Snow crabs (*Chionoecetes opilio* O. Fabr.) off the Gulf of St. Lawrence. Int. Symp. King & Tanner Crabs, Nov. 1989, Anchorage, Alaska pp 193-205.

Brown, R.B. and Guy C. Powell, 1972. Size at maturity in male Alaskan Tanner crab, *Chionoecetes bairdi*, as determined by chela allometry, reproductive tract weights, and size of precopulatory males. J. Fish. Res. Board Can., Vol. 29, No. 4:423-427.

Caddy, J.F., and J.A. Gulland, 1983. Historical patterns of fish stocks. Mar. Policy 10. pp.267-278

Caddy, J.F., and R. McGarvey, 1996. Targets or limits for management of fisheries?. N. Am. J. Fish. Management 16: 479-487.

CAFSAC 1989. Advice on the management of snow crab, Canadian Atlantic Fisheries Scientific Advisory Committee Advisory Document 89/2

Childress, J.J. 1971a. Respiratory rate and depth of occurrence of mid-water animals. Limnol. Oceanog. 16:104-106.

Childress, J.J. 1971b. Respiratory adaptations to the oxygen minimum layer in the bathypelagic mysid *Gnathophausia ingens*. Biol. Bull., 141: 109-121.

Colgate, W.A., 1982. A review of the Gulf of Alaska tanner crab, *Chionoecetes bairdi*, fishery and management related research. Alaska Sea-Grant Report 82-10 : 41-70.

Columbia River Estuary and Adjacent Ocean Waters, Bioenvironmental studies 1972. Alverson and Pruter editors. U. of Washington press, Seattle WA. 868pp.

Comeau,M., G.Y. Conan, G. Robichaud and A. Jones, 1991. Life History patterns and population fluctuations of snow crab (*Chionoecetes opilio*) in the fjord of Bonne Bay on the west coast of Newfoundland, Canada - from 1983 to 1990. Can. Tech. Rep. Fish. Aquat Sci. No. 1817.

Conan, G, R. Elner and M. Moriyasu, 1990. Review of the literature on life histories in the genus *Chionoecetes* in light of the recent findings on growth and maturity of *C. opilio* an eastern Canada. Proc. Int. Symp. King & Tanner Crabs. Nov. 1989, Anchorage, Alaska. pp 163-175.

Conan, G.Y and M. Comeau, 1986. Functional maturity and terminal molt of male Snow crab, *Chionoecetes opilio*. Can. J. Fish. Aquat. Sci., Vol. 43 pp 1710-1719.

Conan, G.Y., M.Moriyasu, M. Comeau, P. Mallet, R. Cormier, H. Chiasson, and Y. Chiasson, 1988. Growth and maturation of snow crab (*Chionoecetes opilio*) p.45-66. *In* G.S. Jamieson and W.D. McKone [ed.] Proceedings of the International Workshop on snow crab biology, December 8-10, 1987, Montreal, Quebec. Can. Manuscr. Rep. Fish. Aquat. Sci. 2005

Conan, G.Y., R.W. Elner and M. Moriyasu, 1989. Review of literature on life histories in the genus Chionoecetes in light of the recent findings on growth and maturity of *C. opilio* in eastern Canada. Proc. Int. Symp. King & Tanner Crabs, Nov. 1989, Anchorage, Alaska.

Couch, J.A. and S. Martin, 1979. Protoxoon symbionts and related disease of the blue crab *Callinectes sapidus* Rathbun, from the Atlantic and Gulf coasts of the United States. In Proc. Blue Crab Colloq. Gulf States Marine Fish. Comm., Ocean Springs, MS, pp 71-81.

Dawe, E. A., 1996. Stock status report Newfoundland and Labrador snow crab. DFO SSR 96/ _ : 1-5.

Dawe, E.G., D.M. Taylor, J.M. Hoenig, W.G. Warren, P.G. Ennis, R.G. Hooper, W.E. Diamond, N., and D.G. Hankin, 1985. Movements of adult female Dungeness crabs (*Cancer Magister*) in northern California based on tag recoveries. Can. J. Fish. Aquat. Sci., 42:919-926.

Donaldson, A.J. Paul and J.M. Paul, 1991. A critical look at the idea of terminal molt in male snow crab (*Chionoecetes opilio)* . Can . J. Fish. Aquat. Sci. Vol. 48(11) 2266-2275.

Donaldson, A.J. Paul and J.M. Paul, 1991. A critical look at the idea of terminal molt in male snow crab (*Chionoecetes opilio*). Can. J. Fish. Aquat. Sci. Vol. 48(11) 2266-2275.

Donaldson, W.E. 1980. Movements of tagged male tanner crabs, *Chionoecetes bairdi*, liberated off Kodiak Island, Alaska. Alaska Dept. of Fish and Game information leaflet No. 188, 60p.

Donaldson, W.E. and A.E. Adams, 1989. Ethogram of behaviour with emphasis on mating for the tanner crab *Chionoecetes bairdi* Rathbun. J. Crustacean Biology 9: 37-53.

Donaldson, W.E. and A.E. Adams,1986. An ethogram and description of mating behaviour for the Tanner crab, *Chionoecetes bairdi* M.J. Rathbun. Alaska Dept. of Fish and Game Information leaflet No. 256, 30p.

Donaldson, W.E., R.T. Cooney, and J.R. Hilsinger, 1881. Growth, age and size at maturity of Tanner crab, *Chionoecetes bairdi* M.J. Rathbun, in the northern Gulf of Alaska (Decapoda, Brachyura). Crustaceana 40 (3) : 286-302.

Eaton, B., C. Botelho. K. Imamura and T. Meyers ,1989. Preliminary results on the seasonability and life cycle of the parasitic dinoflagelate causing bitter crab

disease in Tanner crabs. Proc. Int. Symp. King & Tanner Crabs, Nov. 1989, Anchorage, Alaska pp. 407-408.

Eggleston, D.B. and D.A. Armstrong, 1995. Pre and post-settlement determinants of estuarine Dungeness crab recruitment. Ecological monographs. 65(2) : 193-216.

Elner, R, W. and D. A. Robichaud, 1986. Assessment of the fishery for snow crab off the Atlantic coast of Cape Breton Isl. In 1985. Can. Atl. Fish. Sci. Adv. Council Res. Doc. 86:10, 30 pp.

Elner, R. W., and P.G. Beninger, 1992. The reproductive biology of snow crab *Chionoecetes opilio*: A synthesis of recent contributions. Amer. Zoo., 32: 524-533.

Elner, R. W., and P.G. Beninger, 1995. Multiple reproductive strategies in snow crab *Chionoecetes opilio*: Physiological pathways and behavioral plasticity. J. Exp. Mar. Biol. Ecol. 193 : 93-112

Elner, R.W. and D.A. Robichaud, 1983. Observations on the efficacy of the minimum legal size for Atlantic snow crab *Chionoecetes opilio*. Can. Atl. Fish. Sci. Adv. Comm. Res. Doc. 83(63): 17 pp.

Ennis, G.P. , R.G. Hooper, and D.M. Taylor, 1988. Functional maturity in small male snow crabs (*Chionoecetes opilio*). Can. J. Fish. Aquat. Sci. Vol. 45(12) 2106-2109.

Ennis, G.P., R.G. Hooper, and D.M. Taylor, 1990. Changes in the composition of snow crab (*Chionoecetes opilo*) participating in the annual breeding migration in Bonne Bay, Newfoundland. Can. J. Fish. Aquat. Sci. Vol. 47(11) 2242-2249.

FAO 1995. Precautionary approach to fisheries. Part I: Guidelines on the precautionary approach to capture fisheries and species introductions. Elaborated by the Technical Consultation on the Precautionary Approach to Capture Fisheries (including species introductions). Lysekil, Sweden, 6-13 June 1995. FAO Fish. Tech. Pap. 350, Part I. 47p.

Favorite, F.A., A.J. Dodimede, and K. Nasu, 1976. Oceanography of the Subarctic Pacific region, 1960-1971. Int. North Pac. Fish. Comm., Bull. 33, 187p.

Fernandez, M., D. Armstrong, and O. Iribarne, 1993. First cohort of young-of-the-year Dungeness crab, *Cancer magister*, reduces abundance of subsequent cohorts in intertidal shell habitat. Can. J. Fish. Aquat. Sci, Vol. 50, 2100-2105.

Field, R.H., C.J. Chapman, A.C. Taylor, D.M. Neil, and K. Vickerman, 1992. Infection of the Norway lobster *Nephros norvegicus* by a Hematodynium-like species of dinoflagelate on the west coast of Scotland. Dis. Aquat. Org. 13:1-15.

Foyle, T.P., R.K. O'Dor, and R.W. Elner, 1989. Energetically defining the thermal limits of the snow crab. J. exp. Biol. 145: 371-393.

Freeland, H.J., W.R. Crawford and R.E. Thomson, 1984. Currents along the Pacific coast of Canada. Atmosphere -Ocean 22 (2) 151-172.

Fukataki, H. Number of ovarian eggs of the deep sea edible crab, *Chionoecetes japonicus* Rathbun, in the Japan Sea. Bull. Jap. Sea. Reg. Fish. Lab. 15: 95-97. J. Fish. Res. Bd. Can. Trans. Series. 1192.

Gage, J.D. 1991. Biological rates in the deep sea: A perspective from studies on processes in the benthic boundary layer. Rev. Aquat. Sci 5: 49-100.

Gage, J.D. 1993. Recruitment and age structure of deep-sea invertebrate populations. in:. Reproduction, larval biology and recruitment of the deep sea benthos. Young, C.M., and K.J. Eckelbarger, Columbia University Press, New York, 336p.

Garcia, S.M. 1994. The precautionary principal: its implications in capture fisheries management. Oceans and Coastal Management 22: 99-125.

Gillespie, G.E. 1993. An updated list of the fishes of British Columbia, and those of interest in adjacent waters, with numeric code designations. Can. J. Fish. Aquat. Sci. Tech. Rep. 1918, 116p.

Gooding, R.M. 1985. Predation on released spiny lobster, *Panuliris marginatus*, during tests in the northwestern Hawaiian Islands. Mar. Fish. Rev. 47: 27-35.`1

Gotshall, D.W. 1978. Northern California Dungeness crab *Cancer magister*, movements as shown by tagging. Cal. Fish. Game 64(4) : 234-254.

Hare, G.M. and D.L. Dunn. 1993. A retrospective analysis of the Gulf of St. Lawrence snow crab (*Chionoecetes opilio*) fishery 1965-1990, p 177-192. *In* L.S. Parsons and W.H. Lear [eds]. Perspectives on Canadian Marine fisheries management. Can. Bull. Fish. Aquat. Sci. 226

Hart, J.F.L. 1982. Crabs and their relatives of British Columbia. B.C. Prov. Museum Hdbk. 40: 266p.

Hartnol, R.G. 1978. The determination of relative growth in crustacea. Crustaceana 34:281-293.

Hastie, L.C. 1995. Deep-water Geryonid crabs: a continental slope resource. Oceanography and Marine Biology: an Annual Review 1995, 33, 561-584.

Haynes, E., J.F. Karinen, J. Watson and D.J. Hobson, 1976. Relation of number of eggs and egg length to carapace width in the Brachiuran Crabs *Chionoecetes bairdi* and *C. opilio* from the southeastern Bering sea and *C. opilio* from the Gulf of St. Lawrence. J. Fish. Res. Board Can., Vol. 33: 2592-2595.

Haynes, E., 1973. Descriptions of prezoea and stage I zoea of *Chionoecetes bairdi* and *C. opilio* (Oxyrhyncha, majidae). Fish Bull. U.S. 71: 769-775.

Haynes, E. 1981. Description of stage II zoea of snow crab, *Chionoecetes bairdi* (Oxyrhyncha, majidae) from plankton of lower Cook Inlet, Alaska. Fish.Bull. U.S.: 79, No. 1, 1981.

Hibbits, J., G.H. Hughes, and A.E. Sparks, 1981. *Trichomaris invadens* gen. et sp. nov., an ascomycete parasite of the tanner crab (*Chionoecetes bairdi* Rathbun Crustacea; Brachyura). Can. J. Bot. 59: 2121-2128.

Hicks, D.M., 1982. Abundance and distribution of black mat syndrome on stocks of tanner crabs, *Chionoecetes bairdi*, in the northwestern Gulf of Alaska. In. Proceedings of the International Symposium on the Genus Chionoecetes. Alaska Sea Grant Rep. 82-10

Hilborn, R. 1987. Living with uncertainty in resource management. N. Am. J. Fish. Management 7: 1-5.

Hilborn, R. and C.J. Walters, 1992. Quantatative Fisheries Stock Assessment: choice, dynamics, and uncertainty. Chapman and Hall, London. 570p.

Hilborn, R. and J. Sibert ,1988. Adaptive management of developing fisheries. Mar. Policy (4) 112-121.

Hoenig, J.M. E.G. Dawe and P.G. O'keef, 1994. Molt indicators and growth per molt for male Snow crabs (*Chionoecetes opilio*). Journal of Crustacean Biology, 14:(2) 273-279.

Hoenig, J.M. 1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull., U.S. 81: 898-903.

Hooper, R.G. 1986. Spring breeding migration of the snow crab *Chionoecetes opilio* (O. fabr.) into shallow water in Newfoundland. Crustaceana 50: 257-264.

Hudson, D., N. Hudson and J.D. Shields, 1993. Infection of Trappezia sp.(Decapoda: Xanthidae) by hematodynium sp. (*Duboscquodinida*: *Syndinidae*): A new family record of infection. J. Fish. Dis. 16: 273-276.

Hughes, S.E. 1981. Initial U.S. exploration of nine Gulf of Alaska Sea mounts and their associated fish and shellfish resources. Mar. Fish Rev. 43(1):26-33.

Incze, L.S. and D.A. Armstrong, 1987. Abundance of larval tanner crabs (Chionoecetes spp.) in relation to adult females and regional oceanography of the southeastern Bering Sea. Can.J.Fish. Aquat. Sci. 44:1143-1156.

Jamieson, G.S. 1990. Development of a fishery for *Chionoecetes tanneri* on the continental slope off British Columbia: Management considerations. Proc. Int. Symp. King & Tanner Crabs, Nov. 1989, Anchorage, Alaska.

Jamieson, G.S., C.K. Robinson, and T.H. Butler, 1986. King and tanner crabs in northern British Columbia mainland inlets, May 4 - June 18, 1982. Can. Manuscript. Rep. Fish. Aquat. Sci. No. 1880; 127p

Jamieson, G.S., G.D. Heritage and N. Noakes, 1990. Life history characteristics of *Chionoecetes tanneri* off British Columbia. Proc. Int. Symp. King & Tanner Crabs. Nov. 1989, Anchorage, Alaska.

Jewett, S.C. 1982. Predation on crabs of the Genus Chionoecetes: a literature review. Proc. Int. Symp. on the Genus Chionoecetes; Alaska Sea Grant Rep; 82-10

Jewett, S.C. and H.M. Feder, 1982. Food of the tanner crab, *Chionoecetes bairdi* near Kodiak Island, Alaska. In Proc. Int. Symp. on the Genus Chionoecetes; Alaska Sea Grant Rep; 82-10

Kanno, Y. 1987. Reproductive ecology of tanner crab in the south western Okhotsk Sea. In: Nippon Suisan Gakkaishi, Vol. 53, No. 5: 733-738. Can. Transl Fish Aquat. Sci No. 5628.

Katoh, G., I. Yamanaka, A. Ochi, and T. Ogata, 1965. General aspects on trawl fisheries in the Japan Sea (in Japanese with English summary). Bull. Jap. Sea. Reg. Fish Res. Lab. 4: 1-331.

Kon, T. Niwa, M. and F.Yamakawa, 1968. Fisheries biology of the tanner crab. II On the frequency of molting. Bull. Japanese Soc. Sci. Fish. Vol. 34, No. 2: 138-142. Fish Res. Board Can. Translation Series No. 1129.

Kon, T.,1980. Studies on the life history of the Zuwai crab *Chionoecetes opilio* (O.Fabricius). Spec. Publ. Sado Mar. Biol. Stn. Niigata Univ. Series. No. 2: 1-64. [Can. Transl. Fish. Aquat. Sci. No. 5634.].

Kon, T., N. Letsugu, and H. Kinoshita, 1993. The composition of molting stages in the snow crab *Chionoecetes opilio* caught off Wakasa Bay, the Sea of Japan. Nipon Suisan Gakkaishi, 59:1831-1836 [Can. Transl. Fish. Aquat. Sci. No. 5626].

Kruse, G.H. 1993. Biological perspectives on crab management in Alaska. Proc. Int. Symp. on Management strategies for exploited fish populations. Alaska Sea Grant College Program, 93-02 355-384

Kruse, G.H. 1996. Crab research in Alaska: An interagency long-term plan. Proc. Int. Symp. Biology and Management and economics of crabs from High Latitudes; U of Alaska Sea Grant , Rep. No. 96-02.

Kuris, A.M., S.F. Blau, A.J. Paul, J.D. Shields, and D.E. Wickham, 1991. Infestation by brood symbionts and their impact on egg mortality of the red king crab *Paralithodes camtschatica*, in Alaska: Geographic and temporal variation. Can. J. Fish Aquat. Sci. 48: 559-568.

Leaman, B.M., 1991. Reproductive styles and life history variables relative to exploitation and management of *Sebastes* stocks. Environ. Biol. Fishes 30: 253-271.

Lefebvre, L and J Brethes, 1990. Food of early benthic stages of Snow crab (*Chionoecetes opilio*) in the southwestern Gulf of ST. Lawrence. Proc. Int. Symp. King & Tanner Crabs, Nov. 1989, Anchorage, Alaska pp 273-282.

Lough, R.G. 1974. Dynamics of crab larvae (Anomura, Brachyura) off the central Oregon coast, 1969-1971. Ph.D. thesis, Oregon State U. , Coprvalis, 299 p.

Love, D., R. Thomas and A. Moles, 1996. Bitter crab hemolymph studies: Indications of host physiological condition. Proc. Int. Symp High Latitude Crabs; Alaska Sea Grant 96-02:549-562

Love, D.C., S.D. Rice, D.A. Moles and W.D. Eaton, 1993. Seasonal prevalence and intensity of bitter crab dinoflagelate infection and host mortality in Alaskan tanner crabs *Chionoecetes bairdi* from Auke Bay, Alaska, USA. Dis. Aquat. Org. 15:1-7.

Lovrich, G.A., B. Sainte-Marie, and B.D. Smith, 1995. Depth distribution and seasonal movements of *Chionoecetes opilio* (Brachyura: Majidea) in Baie Sainte-Marguerite, Gulf of St. Lawrence. Can. J. Zoo. 73: 1712-1726.

MacArthur, R.H. and E.O. Wilson, 1967. The theory of island biogeography. Princeton University press, NJ.

Mace, P.M. 1994. Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. J. Fish. Aquat. Sci., 51: 110-122.

MacIntosh, R.A., B.G. Stevens, J.A. Haaga and B.A. Johnson, 1996.InProc. Int. Symp. on biology, management and economics of high latitude crabs. Alaska Sea Grant Rep. 96-02.577-590.

MacLean, S.A. and C.L. Ruddell, 1978. Three new crustacean hosts for the parasitic dinoflagellate *Hematodinium perizi* (Dinoflagellata: Syndinidae). J. Parasite. 64: 158-160.

Mallet, P., G.Y. Conan, and M. Moriyasu, 1993. Periodicity of spawning and duration of incubation time for *Chionoecetes opilio* in the Gulf of St. Lawrence. Int. Council Explor. Sea, CM 1993/K26, 17 pp.

Marshal, N.B. 1954. Aspects of deep sea biology. Huchinsons, 380 p.

McBride, J. 1982. Tanner crab tag development and tagging experiments 1978-1982. Alaska Sea-Grant Report 82-10 : 385-403.

McDaniels, T. 1996. Report on workshop for managers on risk averse/precautionary fisheries management. DFO internal document, 26 pp.

McLeese, D.W. 1968. Temperature resistance of the spider crab *Chionoecetes opilio*. J. Fish. Res. Bd. Canada, 25(8): 1733-1736.

McLeese, D.W. and J. Watson, 1968. Oxygen consumption of the spider crab (*Chionoecetes opilio*) and the American lobster (*Homarus americanus*) at a low temperature. J. Fish. Res. Bd. Can. 25: 1729-1732.

Methodology Manual: Measurement of fishing gear selectivity. Special report prepared for the Dept. of Fisheries and Oceans, Fisheries Management, Ottawa, Canada 1995.

Meyers, T. R., D.V. Lightener, and R.M. Redman, 1994. A dinoflagelate-like parasite in Alaskan spot shrimp *Pandalus platycerus* and pink shrimp *P. borealis*. Dis. Aquat. Org. 18: 71-76.

Meyers, T., B. Eaton, S. Short, C. Botelho, T. Koenman, A. Sparks and F. Morado, 1990. Bitter crab dinoflagelate disease: Overview of the causative agent and its importance and distribution in the Alaskan Tanner crab (*Chionoecetes bairdi, C. opilio*) fisheries. (abstract) Int. Symp. King & Tanner Crabs, Nov. 1989, Anchorage, Alaska p.405.

Miller, R.J. and R.W. Elner, 1993. A good times licensing strategy for limited entry fisheries. North American Journal of Fisheries Management 13: 387-390

Miller, R.J. and J. Watson, 1976. Growth per molt and limb regeneration in the Spider Crab *Chionoecetes opilio*. J. Fish Res. Board Can., Vol. 33, pp. 1644 - 1649.

Miller, R.J. and P O'Keefe, 1981. Seasonal and depth Distribution, size and molt cycles of the spider crabs, *Chionoecetes opilio, Hyas araneus and Hyas coarctatus* in a Newfoundland Bay. Can. Fish. Aquat. Sci. tech. Rep. 1003.

Mohn, R. 1988. Generic dynamic and production models for snow crab *Chionoecetes opilio* In Proc. Int. workshop on snow crab biology. Can. MS Rep. Fish. Aquat. Sci. 2005 : 132-144.

Moriyasu, M., and G.Y. Conan, 1988. Aquarium observations on mating behaviour of snow crab, *Chionoecetes opilio*. Int. Council. Explor. Sea C.M. K:9.

Moriyasu, M., G.Y. Conan, P. Mallet, Y.G. Chaisson and H. Lacroix, 1987. Growth at molt, molting season and mating of snow crab (*Chionoecetes opilio*) in relation to functional maturity. Int. Cons. Exp. Sea, Abstracts, Vol. 2

Moriyasu. M. and P. Mallet, 1986. Molt stages of the snow crab *Chionoecetes opilio* by observation of morphogenesis of setae on the maxilla. Journal of Crustacean Biology, 6(4) : 709-718.

Motoh, H. 1978. The larval stages of the genus Chionoecetes: *C. opilio* and *C. japonicus* reared in the laboratory. In Proc. Int. Symp. on the Genus Chionoecetes. Alaska Sea Grant Rep. 82-10 137-156. U. of Fairbanks, Alaska.

Murie, D.J., W. Mitton, M.W. Saunders and G.A. McFarlane, 1995. A summary of Sablefish tagging and biological studies conducted during 1982-1987 by the Pacific Biological Station. Can. J. Fish Aquat. Sci. Tech. Rep. 959. 84p.

Murphey, M.C. and G.H. Kruse, 1995. An annotated bibliography of capture and handling effects on crabs and lobsters. Alaska Fishery Research Bulletin 2(1): 23-75.

Murphy, G.I. 1968 Pattern in life history and the environment. Am. Nat 102: 391-403.

National Marine Fisheries Service. 1993. Manual of crab sampling methods for the trawl survey in the eastern Bering Sea, 1993. Alaska Fisheries Science Centre, Kodiak, AK, 18 pp

Nevissi, A., J.M. Orensanz, A.J. Paul and D.A. Armstrong, 1996. Radiometric estimation of shell age in Chionoecetes spp. from the eastern Bering Sea, and its use to interpret shell condition indices: preliminary results. In: Proc. Int. Symp. on the Biology and Management of Crabs from High Latitude Habits. Lowell Wakefield Fisheries Symposium, Anchorage Alaska.

Newman, N.W. and C.A. Johnson, 1985. A disease of blue crabs (*Callinectes sapidus*) caused by a parasitic dinoflagelate, *Hematodinium* sp. J. Parasitology. 61: 554-557.

Nizyaev, S.A. and V.Y. Fedoseev, 1996. Causes of reduction in crab brood abundance and role in reproductive strategy. in Proc. Int. Symp. on Biology, Management and Economics of Crabs from High Latitude Habits. University of Alaska Sea Grant College Rpt. No. 96-02 Anchorage, pp. 365-381.

O'Halleran and R.K. O'Dor, 1988. Molt cycle of male snow crabs, *Chionoecetes opilio*, from observations of external features, setal changes, and feeding behaviour. Journal of Crustacean Biology, 8(2): 164-176.

Paul, A.J. and A. Fuji, 1989. Bioenergetics of the Alaskan crab *Chionoecetes bairdi* (Decapoda: Majidae). J Crust. Biol. 9: 25-36.

Paul, A.J. and J.M. Paul, 1989. The size at the onset of maturity in male *Chionoecetes bairdi* (Decapoda, Majidae). Proc. Int. Symp. King & Tanner Crabs. Nov. 1989, Anchorage, Alaska. pp 95-103.

Paul, A.J. and J.M. Paul, 1992. Second clutch viability of *Chionocetes bairdi* Rathbun (Decapoda: Majidae) inseminated only at the maturity molt. Journal of Crustacean Biology, 12(3): 438-441.

Paul, A.J. and J.M. Paul, 1995. Molting of functionally mature male *Chionoecetes bairdi* Rathbun (Decapoda: Majidae) and changes in carapace and chela measurements. J. Crustacean Biology, 15(4): 686-692.

Paul, A.J. and J.M. Paul, 1996. Observations on mating of multiparous *Chionoecetes bairdi* Rathbun (Decapoda: Majidae) held with different sizes of males and one clawed males. J. Crustacean Biology 16(2): 295-299.

Paul, A.J. and J.M. Paul, 1995. Changes in carapace lengths in mature male red king crabs *Paralithodes camtchaticus* after molting in the laboratory. Alaska Fishery Research Bulletin 2(2): 164-167.

Paul, A.J. 1984. Mating frequency and viability of stored sperm in the Tanner crab *Chionoecetes bairdi* (Decapoda: Majidae). J. Crust. Biol. 4: 375-381.

Paul, A.J., H.M. Feder and S.C. Jewett, 1979. Food of the snow crab, *Chionoecetes bairdi* Rathbun, 1924, from Cook Inlet, Alaska (Decapoda: Majidae). Crustaceana, Suppl. 5: 62-68.

Pereyra, W. T. 1968. Distribution of juvenile tanner crabs (*Chionoecetes tanneri* Rathbun) life history model, and fisheries management. Proc. Nat. Shellfisheries Ass. Vol. 58: 66-70.

Pereyra, W.T. 1967. The bathymetric and seasonal abundance and general biology of the Tanner Crab, *Chionoecetes tanneri* Rathbun (Brachiura: Majidae), off the northern Oregon coast. Ph.D. thesis, University of Washington, Seattle, 415 p.

Pereyra, W.T. 1967. The bathymetric and seasonal abundance and general ecology of the tanner crab, *Chionoecetes tanneri* Rathbun (Brachyura: Majidae) off the northern Oregon coast. *In* A. T. Pruter and D. L. Alverson (editors), Columbia river estuary and adjacent ocean waters: Bioenvironmental studies, p. 538-582.

Pereyra, W.T. 1965. Carapace length-width relationships for male and female Tanner crab. Trans. Am. Fish. Soc., Vol. 94, No. 3: 269-270.

Pereyra, W.T. 1966. The bathymetric and seasonal distribution , and reproduction of adult Tanner crabs, *Chionoecetes tanneri* Rathbun (Brachyura Majidae), off the northern Oregon coast. Deep Sea Research Vol. 13: 1185-1205.

Perry, I.R., C.J. Walters and J.A. Boutillier, 1999. A framework for providing scientific advice for the management of new invertebrate fisheries. Rev. Fish. Biol. and Fisheries (in press).

Powles, H. 1968. Distribution and Biology of the spider crab *Chionoecetes opilio* in the Magdalen Shallows, Gulf of St. Lawrence. J. Fish Res, Board Can. MS. Rep No. 1003.

Quin, T.J., R. Fagen, and J. Zheng, 1990. Threshold management policies for exploited fish populations. Can. J. Fish Aquat. Sci. 47: 2016-2029.

Rathbun, M.J., 1925. The spider crabs of America. Bull U.S. Natl. Mus. 129, 613 p.

Rice, J., R.D. Humphreys, L. Richards, R. Kadowaki, D. Welch, M. Stocker, B. Turris, G.A. McFarlane, F. Dickson, and D. Ware, 1995. Pacific Stock Assessment Review Committee Annul Report for 1994. Appendix 3. Biological objectives working group report. Can. MS. Rep. Fish. Aquat. Sci. 2318: 16-52.

Robichaud, D.A., R.F.J. Bailey, and R.W. Elner, 1989. Growth and distribution of snow crab, *Chionoecetes opilio*, in the southeastern Gulf of St. Lawrence. J. Shellfish Res. 8: 13-23

Safran, E.B., T.P. Foyle, and R.W. Elner, 1990. Prospects for distinguishing morphometrically mature and immature crabs: an alternative management strategy for the snow crab fishery. CAFSAC Research Document 90/30: 22p.

Sagi, A., J.S.B. Ahl, H. Danae, and H. Laufer 1994. Methyl farnesoate levels in male spider crabs exhibiting active reproductive behaviour. Hormones and Behaviour 28:261-272.

Sainte-Marie, B. and G.A. Lovrich, 1994. Delivery and storage of sperm at first mating of female *Chionoecetes opilio* (Brachyura: Majidae) in relation to size and morphometric maturity of male parent. J. Crustacean Biol. 14: 508-521.

Sainte-Marie, B. 1993. Reproductive cycle and fecundity of primiparous and multiparous female snow crab, *Chionoecetes opilio*, in the northwest Gulf of Saint Lawrence. Can. J. Fish. Aquat. Sci., Vol. 50, 2147-2156.

Sainte-Marie, B. and C. Carriere, 1995. Fertilization of the second clutch of eggs of snow crab, *Chionoecetes opilio*, from females mated once or twice after their molt to maturity. Fishery Bulletin Vol. 93, No.4, 759-764.

Sainte-Marie, B. and F. Hazel, 1992. Moulting and mating of snow crabs, *Chionoecetes opilio* (O. Fabricius), in shallow waters of the northwestern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 49: 1282-1293.

Sainte-Marie, B., J Sevigny, B. Smith and G. Lovrich, 1996. Recruitment variability in Snow crab (*Chionoecetes opilio*): patterns, possible causes and implications for fishery management. in Proc. Int. Symp. on Biology, Management and

Economics of Crabs from High Latitude Habits. University of Alaska Sea Grant College Rpt. No. 96-02 Anchorage, p. 451-478.

Sainte-Marie, B., Jean-Marie Sevigny and Yves Gauthier, 1997. Laboratory behaviour of adolescent and adult males of the snow crab (*Chionoecetes opilio*) Brachyura: Majidae) mated noncompetitively and competitively with primiparous females. Can. J. Fish. Aquat. Sci. 54: (2) 239-248.

Sainte-Marie, B., S. Raymond and J Brethes, 1995. Growth and maturation of the benthic stages of male snow crab, *Chionoecetes opilio* (Brachiura Majidae). Can J. Fish Aquat. Sci. Vol. 52: 903-924.

Shields, J.D. 1992. Parasites and symbionts of the crab *Portunus pelagicus* from Moreton Bay, Eastern Australia. J. Crust. Biol. 12 (1): 94-100.

Shields, J.D., D.E. Wickham, S. F. Bleu, and A. Kuris 1990. Some implications of egg mortality caused by symbiotic nemerteans for data acquisition and management strategies of red king crabs Paralithodes camtschatica. Proc. Int. Symp. King and Tanner Crabs. Alaska Sea Grant Rep. N0. 90-04:383-395.

Sinoda, M. 1982. Fisheries for the genus Chionoecetes in the Southwest Japan Sea. *In* Proceedings of the international symposium on the genus Chionoecetes, p. 21-39 Alaska Sea Grant Rep. 82-10

Sissenwine, M.P. and J.G. Shepherd, 1987. An alternative perspective on recruitment overfishing and biological reference points. Can. J. Fish. Aquat. Sci. 44: 913-918.

Slizkin, A.G. 1989. Tanner crabs (*Chionoecetes opilio, C. bairdi*) of the northwest Pacific: distribution, biological peculiarities and population structure. Proc. Int. Symp. King & Tanner Crabs. Nov. 1989, Anchorage, Alaska. pp 27-32.

Smith, B.D., and G.S. Jamieson, 1991. Movement and spatial distribution, and mortality of male and female Dungeness crab *Cancer magister* near Tofino, British Columbia. Fish. Bull. US. 89: 137-148.

Smith, M.S., M.W. Saunders and W.T. Andrews, 1996. Cruise details of Sablefish (*Anoplopoma fimbria*) surveys conducted in B.C. waters 1988-1993. Can.J. Fish. Aquat. Sci. Tech. Rep. 976; 129p.

Solving Bycatch: Considerations for Today and Tomorrow, 1996. Alaska Sea Grant College Program Report No. 96-03. University of Fairbanks, Alaska.

Somerton, D.A. 1980. Regional variation in the size of maturity of two species of tanner crab (*Chionoecetes bairdi* and *C. opilio*) in the eastern Bering Sea, and its use in defining management subareas. Can. J. Fish. Aquat. Sci., Vol. 38:163-174.

Somerton, D.A. 1982. Estimating the frequency of molting in adult male *C. bairdi* in the eastern Bering Sea. 1982 Symposium

Somerton, D.A. 1981. Contribution to the life history of the deep-sea king crab, *Lithodes couesi*, in the gulf cf Alaska. Fishery Bulletin: Vol. 79, No. 2.

Somerton, D.A. 1982. Bipartite breeding: a hypothesis of the reproductive pattern in tanner crabs. Proc. Int. Symp. on the Genus Chionoecetes. Alaska Sea Grant Rep. 82-10 : 283-292.

Somerton, D.A., and W. Donaldson, 1996. Contribution to the biology of the grooved and triangle Tanner crabs, *Chionoecetes tanneri* and *C. angulatus*, in the eastern Bering Sea. Fishery Bull. 94:348-357.

Somerton, D.A. and W.S. Meyers, 1983. Fecundity differences between primiparous and multiparous female Alaskan tanner crab (*Chionoecetes bairdi*). Journal of Crustacean Biology, 3(2): 183-186.

Sparks, A.E. 1982a. Observations on the histopathology and probable progression of the disease caused by *Trichomaris invadens*, an invasive ascomycete, in the tanner crab, *Chionoecetes bairdi*. Journal of Invertebrate Pathology 40, 242-254.

Sparks, A.E. 1982b. The Histopathology and possible role in the population dynamics of tanner crab, *Chionoecetes bairdi*, of the fungus disease (black mat syndrome) caused by *Trichomaris invadens*. Proc. Int. Symp. on the Genus Chionoecetes; Lowel Wakefield Fisheries Symposia Series; Alaska Sea Grant Rep. No. 82-10

Sparks, A.K. 1981. An invasive fungus disease of the tanner crab and its aquacultural connotations. Proceedings of the ninth and tenth U.S.-Japan meetings on aquaculture, NOAA Tech. Rep. NMFS 16, 61-67.

Stevens, B, W. Donaldson, J Haaga and E. Munk 1993. Morphometry and maturity of paired Tanner crabs, Chionoecetes bairdi, from shallow and deep water environments. Can. J. Fish. Aquat. Sci., Vol. 50, pp.1504-1516.

Stevens, B.G. and R.A. MacIntosh, 1989. Report to industry on the 1990 Eastern Bering Sea crab survey. Alaska Fisheries Science Center Processed Report 89-18, 47p.

Stevens, B.G. and R.A. MacIntosh, 1990. Report to industry on the 1990 Eastern Bering Sea crab survey. Alaska Fisheries Science Center Processed Report 90-09,

Stevens, B.G., J.A. Haaga, and W.E. Donaldson, 1994. Aggregative mating behaviour of tanner crabs, *Chionoecetes bairdi*. J. Fish. Aquat. Sci. 51: 1273-1280.

Stevens, B.G., R.A. MacIntosh and K.L. Stahl-Johnson, 1988. Report to industry on the 1990 Eastern Bering Sea crab survey. Alaska Fisheries Science Center Processed Report 88-23, 41p..

Takeshita, K. , H. Fujita and S. Kawasaki, 1978. Carapace moire topography in crabs. Bull. Far Seas Fish. Res. Lab.(Shimizu), 16: 115-135.

Tarverdieva, M.I. 1976. Feeding of the Kamchatka king crab, *Paralithodes camtschatica*, and Tanner crabs, *Chionoecetes bairdi* and *Chionoecetes opilio*, in the southeastern part of the Bering Sea. Sov. J. of Mar. Biol. 2: 34-39.

Tarverdieva, M.I. and K. A. Zgurovsky 1985. On food composition of the deep water crab species *Lithodes aequispina* Benedict, and *Chionoecetes tanneri* Rathbun in the Bering and Okhotsk Seas. In Proc. Int. Symp. King Crab. Alaska Sea Grant Rep. 85-12 :319-332.

Taylor, D.M. 1982 . A recent development in tagging studies on snow crabs, *Chionoecetes opilio*, in Newfoundland-Retention of tags through ecdysis. Proc.Int. Symp. On the genus Chionoecetus. Alaska Sea Grant Report # 82-10. P 405-420.

Taylor, D.M. 1985. Biological aspects of the spring breeding migration of Snow crabs, *Chionoecetes opilio* in Bonne Bay Newfoundland. Fishery Bulletin Vol. 83, No. 4.

Taylor, D.M. and W.G. Warren, 1989. The effect of shell condition on male snow crab *Chionoecetes opilio*, weight-width relationships. Proc. Int. Symp. King & Tanner Crabs. Nov. 1989, Anchorage, Alaska. pp 145-152.

Taylor, D.M. 1992. Long term observations on movements of tagged male Snow crabs in Bonavista Bay, Newfoundland. North American Journal of Fisheries Management 12: 777-782.

Taylor, D.M. and P.G. O'Keefe, 1987. Analysis of the snow crab *Chionoecetes opilio* fishery in Newfoundland for 1986. Can. Atl. Fish. Sci. Advis. Com. Res. Doc. 87/57. 26 p.

Taylor, D.M. and W.G. Warren, 1989. The effect of shell condition on male Snow crab, *Chionoecetes opilio*. Weight -width relationships. Proc. Int. Symp. King & Tanner Crabs, Nov. 1989, Anchorage, Alaska.

Taylor, D.M., G.W. Marshal and P.G. O'Keefe, 1989. Shell hardening in Snow crabs *Chionoecetes opilio* tagged in soft-shell condition. North American Journal of Fisheries Management 9: 504-508.

Taylor, D.M., P.G. O'Keefe and C. Fitzpatrick, 1994. A snow crab *Chionoecetes opilio* (Decapoda, Majidae), fishery collapse in Newfoundland. Fishery Bulletin 92:412-419

Taylor, D.M., R.G. Hooper, and G.P. Ennis, 1985. Biological aspects of the Spring breeding migration of snow crabs, *Chionoecetes opilio*, in Bonne Bay, Newfoundland, (Canada). Fish Bull. U.S. 83: 707-711.

Tester, P.A., and A.G. Carey, 1986. Instar identification and life history aspects of juvenile deep water spider crabs, *Chionoecetes tanneri* Rathbun. Fishery Bulletin: Vol. 84, No.4 973-980.

Thompson, R.J. and M Hawryluk, 1989. Physiological energetics of the Snow crab *Chionoecetes opilio*. Int. Symp. King & Tanner Crabs, Nov. 1989, Anchorage, pp 283-291.

Thomson, A. 1989. An Industry perspective on problems facing the rebuilding of King and Tanner (*C.bairdi*) crab stocks of the eastern Bering sea. Proc. Int. Symp. King & Tanner Crabs, Nov. 1989, Anchorage, Alaska pp. 533-546.

Thomson, R.E. 1981. Oceanography of the British Columbia coast. Can. Spec. Publ. Fish. Aquat. Sci. 56: 291p.

Tohshi, K., N. Letsuga, and H. Kinoshita, 1994. The composition of molting stages in the snow crab *Chionoecetes opilio* caught off Wakasa Bay, the Sea of Japan. J. Jap. Soc. Sci. Fish. 59:11 1831-1836.

Tracy, D., 1995. Alaska Department of Fish and Game Summary of the 1994 Mandatory Shellfish Observer Database. Regional Information Report No. 4K95-32. ADF&G, Kodiak.

Tremblay M.J., M.D. Eagles and R.W. Elner, 1994. Catch, effort and population structure in the snow crab fishery off eastern Cape Breton, 1973-1993: a retrospective. Can. Tech. Rep. Fish. Aquat. Sci. 2021. 44p.

Tunnicliffe, V. 1991. The biology of the hydrothermal vents: Ecology and evolution. Oceanogr. Mar. Biol. Ann. Rev. 29: 319-407.

Univ. Of Alaska,1995. Solving Bycatch. Sea Grant College Program. Report. Fairbanks # 96-03

Walters, C.J. 1996. Review of PSARC document on new invertebrate fisheries development, unpublished.

Watson, J. 1969. Biological investigations of the spider crab, *Chionoecetes opilio*. Can. Fish. Rep., 13: 24-47.

Watson, J. 1972. Mating behaviour in the spider crab, *Chionoecetes opilio*. J. Fish. Res. Board Can., Vol. 29, No. 4:447-449.

Watson, J., 1970. Tag recaptures and movements of adult male snow crabs *Chionoecetes opilio* (O. fabricius), in the Gaspe region of the Gulf of St. Lawrence. Fish. Res. Bd. Can. Tech. rep. 204

Watson, J. and P.G. Wells, 1972. Recaptures and movements of tagged snow crabs (*Chionoecetes opilio*) in 1970 from the Gulf of St. Lawrence. Fish. Res. Board of Canada Tech. Rep. 349.

Wickham, D.E. 1979. Predation by the nemertean *Carcinomertes errans* on the eggs of the Dungeness crab *Cancer magister*. Mar. Biol. 55: 45-53.

Wickham, D.E. 1986. Epizootic infestations by nemertean brood parasites on commercially important crustaceans. Can. J. Fish. Aquat. Sci. 43: 2295-2302.

Wickham, D.E. and A. Kuris, 1990. Brood mortality and role of symbiotants in egg mortality of the Tanner crab *Chionoecetes bairdi* in Alaskan waters. Int. Symp. King & Tanner Crabs, Nov. 1989, Anchorage, Alaska pp 397-403.

Witherall, D. 1996. King and Tanner crabs of the Bering Sea and Aleutian Islands Area: Species Profiles. North Pacific Fishery Management Council. Anchorage, Alaska.

Yasuda, T. 1967. Feeding habits of the zawaigani, *Chionoecetes opilio elongatus*, in Wakasa Bay, I: Specific composition of the stomach contents. Bull. Jap. Soc. Sci. Fish. 33: 315-319. Fish Res. Bd. Can. Translation series No. 1111.

Young, C.M., and K.J. Eckelbarger, 1993. Reproduction, larval biology and recruitment of the deep sea benthos. Columbia University Press, New York, 336p.

Zheng, J.,T.J. Quinn II, and G.H. Kruse, 1993. Comparison and evaluation of threshold estimation methods for exploited fish populations, p 267-289. In G. Kruse , D.M. Eggers, R.J. Marasco, C. Pautzke and T. Quinn (eds). Proceedings of the Int. Symp. On Manag. Strat. For Exploited Fish Popl. Alaska Sea Grant College Prog. Peport # 93-02. Univ. Of Alaska, Fairbanks.

Zhoe, S. and T.C Shirley, 1996. Is handling responsible for the decline of the red King crab fishery? Proc. Int. Symp. Biology and Management and economics of crabs from High Latitudes; U of Alaska Sea Grant , Rep. No. 96-02.

OTHER REFERENCES NOT EXPLICITLY CITED IN THE DOCUMENT

Arnqvist, G. and D. Wooster, 1995. Meta-analysis: synthesizing research findings in ecology and evolution. Trends in Ecology & Evolution Vol. 10, No. 6 236-240.

Bouchard, R., J.F. Brethes, G. Desrosiers, and R.F.J. Bailey, 1986. Changes in size distribution of snow crabs (*Chionoecetes opilio*) in the Gulf of St. Lawrence. J. Northwest Atl. Fish. Sci., Vol. 7: 67-75.

Bradley, G. and J.A. Haaga, 1994. Aggregative mating of tanner crabs, *Chionoecetes bairdi*. Can. J. Fish. Aquat. Sci., Vol. 51, 1273-1280.

Elner, R.W. 1882. Characteristics of the snow crab *Chionoecetes opilio*, fishery off Cape Breton Island. Proc. Int. Symp. on the Genus Chionoecetes. Alaska Sea Grant Report 82-10 : 657-680.

Hart, J.F.L. 1960. The larval development of British Columbia Brachyura. II Majidae, subfamily Oregoniinae. Can. J. Zoo. 38: 539-546.

Hartnol, R.G. 1969. Mating in the Brachyura. Crustaceana, 16: 161-181.
Jamieson, G.S. 1993. Marine invertebrate conservation: Evaluation of fisheries over-exploitation concerns. Amer. Zoo., 33: 551-567.
Jamieson, G.S. and W.D. McKone, 1987. Proceedings of the international workshop on snow crab biology, December 8 - 10 1987, Montreal, Quebec. Can. J. Fish. Aquat. Sci. Man. Rep. 2005; 145 p.
Miller, R.J. 1976. North American crab fisheries: regulations and their rationales. Fishery Bulletin: Vol. 74, No. 3
Miller, R.J. 1977. Resource under-utilization in a spider crab industry. Fisheries, Vol.2, No. 3.
Nizyaev, S.A. and V.Y. Fedoseev, 1992. Disorders of the reproductive cycle in crab females of the genus Paralithodes.In Int. Symp. on King and Tanner Crabs. Alaska Sea Grant Rep. 90-04:91-94.
Otto, R.S. 1989. An overview of the eastern Bering Sea king and tanner crab fisheries. Proc. Int. Symp. King & Tanner Crabs. Nov. 1989, Anchorage, Alaska. pp. 9-25.
Pereyra, W.T 1967. Tanner Crab -- An Untapped Pacific Resource. National Fisherman, Vol. 48, No. 4 p 16A.
Schmidt, D.C. and D. Pengilly, 1993. Review of harvest strategies used in the management of Lithodid crab in Alaska. Proc. Int. Symp. Management Strategies of Exploited Fish Populations. Lowell Wakefield Fisheries Symposium, AK-SG-93-02: 385-407.
Somerton, D.A. 1981. Life history and population dynamics of two species of Tanner crab, Chionoecetes bairdi and *C. opilio*, in the eastern Bering Sea with implications for the management of the commercial harvest. Ph.D.. thesis, University of Washington, Seattle, Washington.
University of Alaska Alaska Sea Grant College Prog. Peport # 93-02.1996 Proceedings of the Int. Symp. On Manag. Strat. For Exploited Fish Popl. Univ. Of Alaska, 713 pp.Fairbanks.
University of Alaska Alaska Sea Grant College Prog. Peport # 90-04.1989 Proceedings of the Int. Symp. On King and Tanner Crabs. Univ. Of Alaska, 633pp.Anchorage.
University of Alaska Alaska Sea Grant College Prog. Peport # 85-12.1985 Proceedings of the Int. Symp. On King Crab. Univ. Of Alaska, 507 pp.Fairbanks.